SYSTEMATICS OF ZALUZANIA (ASTERACEAE:HELIANTHEAE)

JOHN S. OLSEN

Zaluzania is a small genus of herbaceous perennials and woody shrubs confined to Mexico, with one taxon disjunct, known only from Ecuador. Members of the genus occupy habitats ranging from 1700 meters altitude in the xeric north central plains to 4000 meters in the mesic mountainous regions of Hidalgo, Mexico, and of Ecuador (Figures 1 & 2). There are no common names for the genus, although two individual taxa have local names; *Z. triloba* is commonly called "hierba amargosa" and *Z. augusta* is called "caxtidani", "cenicillo", "hierba blanca", or "limpia tunas" (Standley, 1926). The genus is usually weedy, with negligible commercial value; however, *Z. triloba* has been shown to produce an antitumor sesquiterpene lactone, zaluzanin C (Jolad et al., 1974).

The present study was undertaken to clarify the taxonomic and phylogenetic relationships among the taxa. Data from cytology, flavonoid chemistry, palynology, geography, and ecology were utilized toward this goal.

GEOGRAPHY AND ECOLOGY

The range of the genus *Zaluzania* covers all of central Mexico, south into Oaxaca and Guerrero, with one taxon in Ecuador. Rzedowski (1973) includes *Zaluzania* in his list of genera primarily concentrated in the dry regions of Mexico, but which are not restricted by the aridity limits. Also included in the list are other Helianthoid genera, *Flourensia, Parthenium,* and *Encelia.* The range of *Zaluzania* is bounded on the west by the Sierra Madre Occidental and stretches eastward into the state of Vera Cruz.

Zaluzania is primarily a summer or fall blooming genus, mostly confined to middle altitudes (1650–2700 meters), commonly occurring in scrub vegetation. Only *Z. megacephala* var. *megacephala* and *Z. sodiroi* occur above 3200 meters. Two of the taxa are wholly xerophytic, the herbaceous *Z. megacephala* var. *coahuilensis* and the shrubby *Z. mollissima,* both being confined to the Chihuahuan Desert flora. Several other species frequent the desert regions, but other populations of the same species are adapted to the more mesic

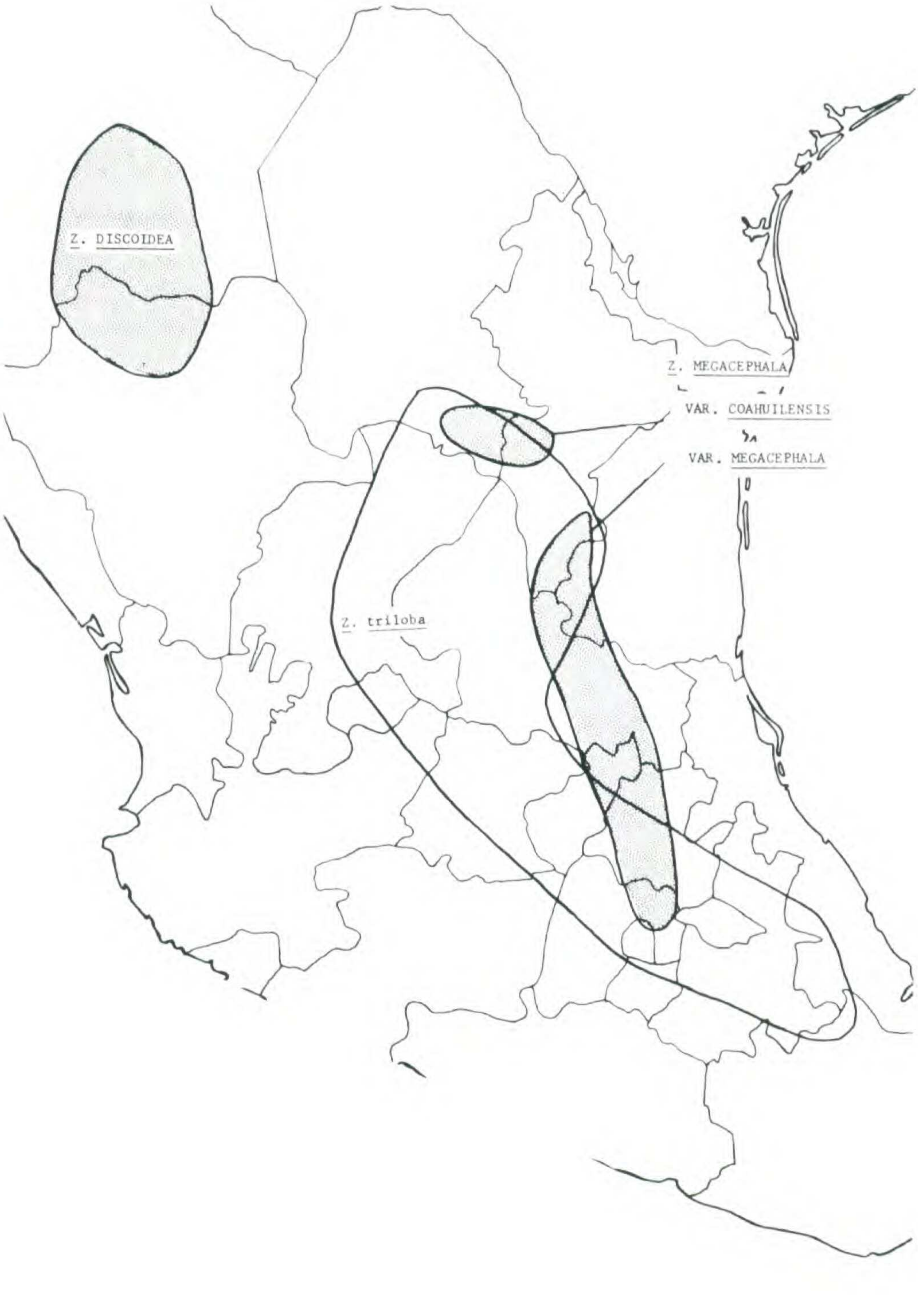

Figure 1. Geographic distribution of the herbaceous members of *Zaluzania*.

central and western areas. *Zaluzania triloba* and *Z. augusta* are typical of this type. Both extend into the Chihuahuan Desert on the north, but also occur in the Valley of Mexico on the south and into Puebla and Vera Cruz on the east. *Zaluzania triloba* is always found growing in the shade of shrubs or cacti in the desert areas. In central Mexico (Guanajuato), *Z. augusta* var. *augusta* often becomes an ecological dominant, at least in terms of biomass. It is frequently seen covering rocky limestone hills, and where it occurs in the Chihuahuan Desert, it is confined to the mountains, where it grows associated with *Agave. Zaluzania discoidea* and *Z. pringlei* occupy mountainous regions in more mesic areas. *Zaluzania pringlei* occurs on limestone hills in Morelos and Guerrero. *Zaluzania discoidea* occurs in Durango and adjacent areas, being especially prominent in areas disturbed by farming. The remaining taxa, *Z. subcordata* and *Z. montagnifolia,* occur in the limestone hills of Puebla, Vera Cruz and Oaxaca.

No pollinators have been identified for any *Zaluzania* taxon, but both beetles and bees have been observed on the flowers. Large grasshoppers have also been observed feeding on the leaves of *Z. augusta* and *Z. montagnifolia.*

TAXONOMIC HISTORY

The genus *Zaluzania* (Asteraceae:Heliantheae) was established in 1807 by Persoon, based on *Anthemis triloba* Ort., a plant widespread in Mexico. In 1816, the genus *Ferdinanda* Lag. was described, including two species, one of which was *F. augusta,* now *Zaluzania augusta.* Kunth described the genus *Chrysophania* in 1832 with *C. fastigiata* as the type species. Since *C. fastigiata* is synonymous with *Z. augusta,* the genus *Chrysophania* passes into synonymy. Robinson and Greenman (1899) retained *Ferdinanda* as a subgenus of *Zaluzania* as did Sharp (1935), the latter relegating 12 taxa to it.

The genus *Hybridella,* based on *Anthemis globosa* Ort., was described by Cassini in 1821. This was treated as a subgenus of *Zaluzania* by Robinson and Greenman (1899) and by Sharp (1935) who included within it two species and one variety.

Zaluzania was treated by Schultz-Bipontinus in 1861 and 1864. In his final assessment of the genus, he included 12 species, six of which

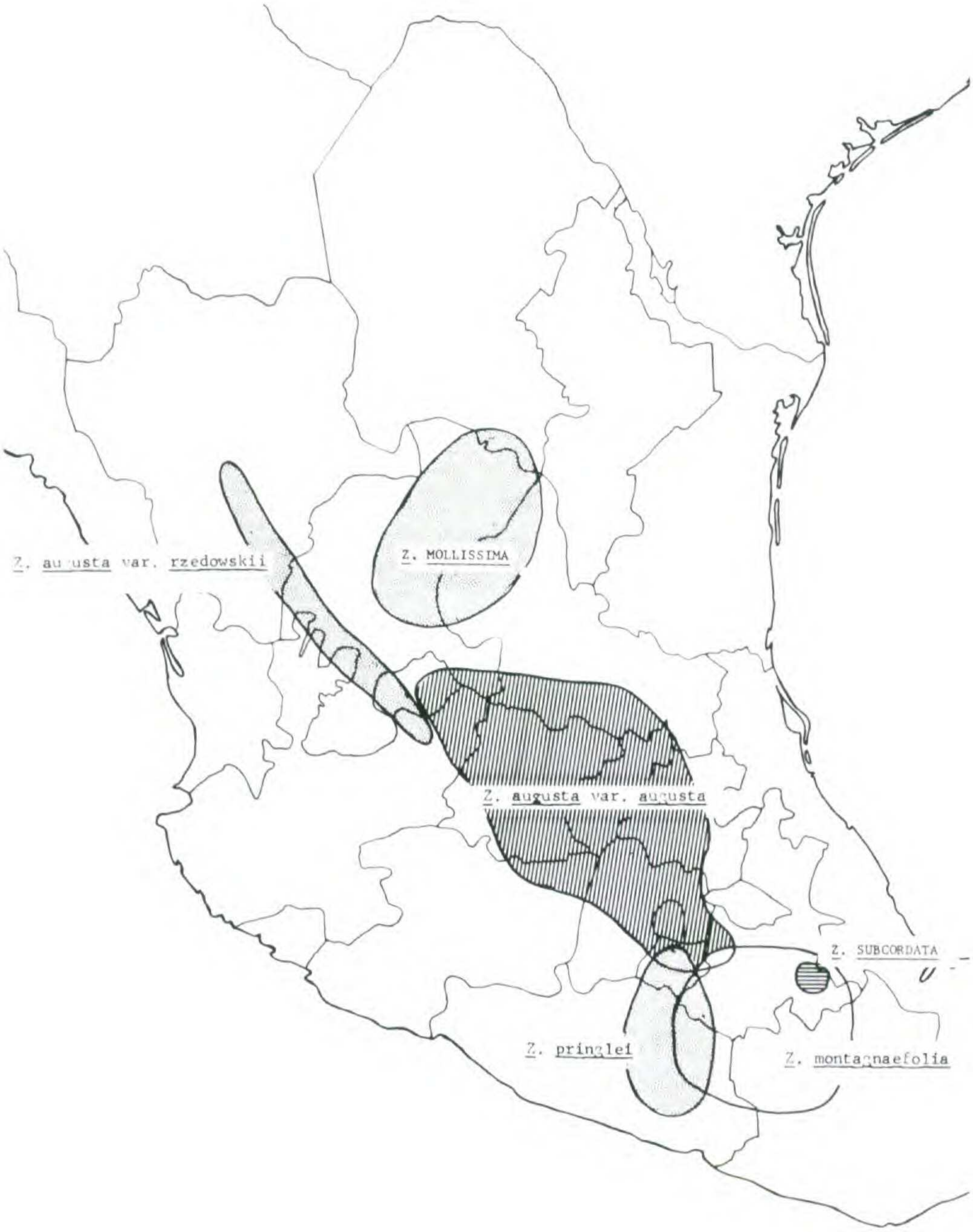

Figure 2. Geographic distribution of the shrubby members of *Zaluzania*, exclusive of *Z. sodiroi*, which is restricted to Ecuador.

are now retained in *Zaluzania*, three referred to *Viguiera*, two to *Hybridella*, and one to *Calea*. Robinson and Greenman published a revision of *Zaluzania* in 1899 in which they recognized 12 species and one variety. Hieronymus (1900) described three new *Zaluzania* taxa from Ecuador, thus extending the range of *Zaluzania* considerably. Sharp (1935) reduced these new taxa to one species, *Z. sodiroi,* and recognized *Zaluzania* as consisting of 14 species and one variety.

More recently, Rzedowski (1968) found *Zaluzania robinsonii* Sharp to be synonymous with the earlier *Aiolotheca parthenioides* DC., thereby making necessary the combination *Z. parthenioides.* McVaugh (1972) added an additional taxon by describing *Z. augusta* var. *rzedowskii. Monactis subdeltoidea,* described by Robinson in 1911 from Ecuadorian material, has been shown to be synonymous with *Z. sodiroi* (Robinson, 1976).

Zaluzania, as recognized in the present treatment, consists of 11 taxa (nine species and two varieties). Table 1 presents a comparison of the present arrangement with the arrangements of Robinson and Greenman (1899) and Sharp (1935). The present system differs from previous ones in several ways. Subgenus *Hybridella,* with its three taxa, has been removed from *Zaluzania* and resurrected to generic rank (Olsen, 1977a) based on differences in habit, morphology and cytology. *Zaluzania grayana,* because of its sterile ray florets and chromosome number of $n = 17$, has been removed from the genus and positioned in the series *Pinnatilobatae* of *Viguiera;* however, it is seemingly also closely related to *Heliomeris* (sensu Yates, 1967) and additional study might suggest a position in this taxon. Finally, *Z. parthenioides* is considered to be conspecific with *Z. triloba.*

GENERIC RELATIONSHIPS

Zaluzania is a homogeneous assemblage of closely knit taxa. Its recognition as a valid genus has not been questioned since its inception. The major taxonomic controversy has been its subtribal position within the tribe Heliantheae.

Persoon (1807) originally placed *Zaluzania* near *Pascalia* and *Spilanthes* (sect. *Acmella*) in the Verbesininae. Cassini (1821) believed that it was misplaced here and put it in his Heliantheae — Milleriees with the genera *Eleutheranthera, Sigesbeckia, Jaegeria, Guizotia,* and *Hybridella.* Of the five latter taxa, *Hybridella* has been moved to a position near *Heliomeris* of the subtribe Helianthinae (Olsen, 1977a); *Eleutheranthera, Sigesbeckia,* and *Jaegeria* were placed in the Verbesininae by Hoffman (1894). Torres (1968) pointed out the close relationship between *Jaegeria* and *Sabazia* of

Table 1

Comparison of Recent Taxonomic Dispositions of Zaluzania Taxa

ROBINSON AND GREENMAN (1899)	SHARP (1935)	OLSEN (1977)
ZALUZANIA	ZALUZANIA	ZALUZANIA
subg. **Ferdinanda**	subg. **Ferdinanda**	
Z. triloba	*Z. triloba*	*Z. triloba* (incl. *Z. robinsonii*)
	Z. robinsonii	
Z. grayana	*Z. grayana*	
Z. coulteri	*Z. cinerascens* (=*coulteri*)	*Z. megacephala* var. *megacephala*
Z. megacephala	*Z. megacephala*	var. *coahuilensis*
Z. discoidea	*Z. discoidea*	*Z. discoidea*
Z. augusta	*Z. augusta*	*Z. augusta* var. *augusta*
		var. *rzedowskii*
Z. mollissima	*Z. mollissima*	*Z. mollissima*
Z. asperrima	*Z. montagnifolia*	*Z. montagnifolia*
var. *montagnifolia*		
	Z. pringlei	*Z. pringlei*
	Z. sodiroi	*Z. sodiroi*
	Z. subcordata	*Z. subcordata*
Z. resinosa		
subg. **Hybridella**	subg. **Hybridella**	HYBRIDELLA (as genus)
Z. globosa	*Z. globosa*	*H. globosa* var. *globosa*
Z. myriophylla	var. *myriophylla*	var. *myriophylla*
Z. anthemidifolia	*Z. anthemidifolia*	*H. anthemidifolia*
	GREENMANIELLA	GREENMANIELLA
	G. resinosa	*G. resinosa*
		Viguiera triloba (=*Z. grayana*)

the Galinsoginae. The position of *Guizotia* is more controversial, its placement being problematical (Baagøe, 1974; Turner & Powell, 1978); in my opinion it is not related to *Zaluzania.*

Bentham (1873) placed *Zaluzania* in the Verbesininae, suggesting that its closest affinities are to the genera *Sabazia* and *Gymnolomia.* As indicated above, *Sabazia* and *Jaegeria* are clearly related. *Sabazia* presumably belongs to the Galinsoginae (Longpre, 1970; Urbatsch & Turner, 1975), along with *Tridax* (Powell, 1965) which would indicate ties to the Galinsoginae for *Zaluzania.*

The situation for *Gymnolomia* is much less clear. Blake (1918), in his monograph of the genus *Viguiera,* reduced *Gymnolomia* from the 30-odd species known to Bentham to only four; he related the latter to *Aspilia* in the Verbesininae. The transferred epappose taxa were distributed among *Viguiera, Tithonia* and *Hymenostephium.*

Robinson and Greenman (1899) made no statements about the generic relationships of *Zaluzania,* but Sharp (1935) placed *Zaluzania* in the Verbesininae noting that "The relationships of *Zaluzania* are with the *Viguiera* complex, but its exact ancestral stock is somewhat in question. Evidence at present points to affinities with a *Viguiera-Gymnolomia* type of ancestor." In short, *Zaluzania* has been related to two quite different subtribes, the Galinsoginae and the Verbesininae.

Stuessy (1978) made some major rearrangements in the subtribal taxonomy of the Heliantheae. He recognized the Verbesininae as distinct from the Helianthinae (containing *Viguiera*) and also erected several new subtribes. *Zaluzania* is placed in one of his new subtribes, the Neurolaeninae, a segregate of the Galinsoginae. Along with *Zaluzania,* the subtribe includes *Bebbia, Clappia, Dyscritothamnus, Greenmaniella, Pseudoclappia, Schistocarpha, Varilla,* and *Neurolaena* itself. This assemblage is characterized by alternate leaves, phyllaries of unequal length (increasing inwards), lanceolate paleae, and setose pappus. Turner and Powell (1978) would fragment Steussy's Neurolaeninae into two subtribes, the Neurolaeninae and the Varillinae; including in the latter, *Clappia, Pseudoclappia, Varilla,* and *Dyscritothamnus.* To this may be added *Bebbia* (Whalen, 1977).

Stuessy referred to the "obvious generic ties . . ." which "exist between *Calea* of the Galinsoginae and *Zaluzania* . . ." of the Neurolaeninae, but felt that inclusion of *Zaluzania* within the

Galinsoginae would result in the expansion of this subtribe beyond the useful limits of, at least his, subtribal concept.

Zaluzania, by my own interpretation, does not fit at all well with the other genera of the Neurolaeninae as circumscribed by Stuessy. It typically is epappose, the phyllaries are nearly equal or decrease in length inwardly and the paleae are not lanceolate, but oblanceolate and trifid. If the Neurolaeninae are ruled out as close relatives, the position of *Zaluzania* is either in the Helianthinae (sensu Stuessy), where Sharp placed it near *Viguiera,* or in the Galinsoginae, where Stuessy placed it near *Calea* and Bentham near *Sabazia.* In my opinion, *Zaluzania* is best placed in the subtribe Helianthinae.

While most of the taxa in the subtribe Helianthinae have neuter ray florets, at least four (*Balsamorhiza, Chromolepis, Vigethia,* and *Wyethia*) have fertile rays (Stuessy, 1978), as does *Zaluzania.* The inflorescence of *Zaluzania* is somewhat more crowded than others in the Helianthinae, but otherwise it fits quite well. The alternate leaves (although occasionally opposite below in the shrubby taxa), black anthers, and lack of glandular pubescence on the corolla tubes clearly distinguish *Zaluzania* from the Galinsoginae.

Calea, with only about 15% of its 85 taxa counted, is multibasic with chromosome numbers of $n = 15, 16, 17, 18, 19,$ and 24 (Beaman & Turner, 1962; Dejong & Longpre, 1963; Keil & Stuessy, 1975; Powell & Cuatrecasas, 1970; Powell & King, 1969; Powell & Turner, 1963[1]; Solbrig et al., 1972; Turner, Ellison & King, 1961; Turner, Powell & King, 1962; Turner, Powell & Watson, 1973), which indicates probable ancestral base numbers of $x = 8$ and 9, with the others derived through aneuploidy. *Viguiera* has chromosome numbers of $n = 12, 17, 18,$ and 32 (Butterwick, 1975; Gupta, Agarwal, & Srivastava, 1972; Heiser, 1963a & b; Heiser & Smith, 1955; Jones, 1970; Powell & Sikes, 1970; Solbrig et al., 1972; Turner & Ellison, 1960; Turner & Flyr, 1966; Turner & King, 1964; Turner, Beaman & Rock, 1961; Turner, Powell & Cuatrecasas, 1967; Turner, Powell & Watson, 1973). Chromosome numbers on a base of $x = 18$ are known in *Viguiera* only in series *Dentatae.*

Chromatographic data indicate that of the various infrageneric taxa of *Viguiera,* the series *Grammatoglossae* shows the closest approach to *Zaluzania* in its flavonoid profiles. *Calea* taxa examined present entirely different profiles.

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[1] *C. urticifolia* is erroneously printed as $n = 9$ in the table from Powell and Turner, 1963. Examination of the voucher (*Johnston 4797,* LL) shows the actual number to be $n = 19$ with a camera lucida drawing appended to the voucher.

Morphologically, series *Grammatoglossae* differs from *Zaluzania* in having, generally, larger and fewer heads, the pales only rarely trifid, and the ray florets all sterile. Cytological knowledge of this 11-species series is limited to three species, all exhibiting $n = 17$. The geographic range of series *Grammatoglossae* overlaps that of *Zaluzania,* but also extends further west into Nayarit. Series *Grammatoglossae* shows a tendency for the tube of the disc corolla to become expanded to form a cap over the achene. This character has previously been considered one of the distinguishing characters of *Zaluzania* (Sharp, 1935). Its presence in series *Grammatoglossae,* while not supporting the distinction, is further indication of the relationship between the two groups.

In short, based on chromosomal, morphological, geographical and chemical data, I believe that *Zaluzania* is best positioned in the Helianthinae, where it is most closely related to *Viguiera.* I would place its connections with section *Chloracra,* possibly with series *Grammatoglossae.*

CYTOLOGICAL STUDIES

Prior to the onset of the present study, chromosome reports were available for only four species of *Zaluzania: Z. augusta* ($n = 18$; Turner & Flyr, 1966), *Z. megacephala* ($n = 16$; Turner, Beaman & Rock, 1961), *Z. montagnifolia* ($n = 18$; Powell & Turner, 1963), and *Z. triloba* ($n = 18$; Powell & Turner, 1963; Turner & Johnston, 1961). Since then, Keil and Stuessy (1975) have reported a count of $n = 17$ for *Z. grayana* (here transferred to *Viguiera*) and Strother (1976) has reported an additional count of $n = 18$ for *Z. triloba.* I have obtained counts of all of these taxa and first reports of five others (Table 2). Vouchers of all counts are deposited in the Lundell Herbarium of the University of Texas (LL).

Chromosome numbers have been determined for over 200 individuals from 60 populations. *Zaluzania* would appear to be monobasic ($x = 18$), with two stabilized polyploid taxa in the genus; however, the series of chromosome numbers present in *Zaluzania* ($n = 18$, 27, & 36) suggests that the ancestral base number for the genus was $x = 9$. This number is one of the presumed base numbers for the Heliantheae as a whole (Stuessy, 1978) and it is possible that *Zaluzania* arose from an $x = 9$ taxon with stabilization occurring at

Table 2

Chromosome numbers in Zaluzania

TAXON	*n*	LOCALITY
		MEXICO:
augusta var. *augusta*	18	**Guanajuato.** 35 mi NE of Guanajuato on Hwy 110 to Dolores Hidalgo. *Olsen 271.*
	18	**Guanajuato.** 6 mi NE of Dolores Hidalgo on Hwy 110. *Olsen 272.*
	18	**Hidalgo.** Along exit road to Tula off Hwy 57. *Olsen 244.*
	18	**Hidalgo.** 10 mi E of Hidalgo-Queretaro border on Hwy 45. *Olsen 284.*
	18	**Hidalgo.** 2.5 mi N of Pachuca on Hwy 105 to Real del Monte. *Olsen 286.*
	18	**Queretaro.** Hwy 57, 2 mi SE of San Juan del Rio. *Olsen 242.*
	18	**Queretaro.** ca 8 mi from Hwy 57 on Hwy 45 to Pachuca. *Olsen 243.*
	18	**Queretaro.** 6 mi S of Vizarron on Hwy 120. *Olsen 283.*
augusta var. *rzedowskii*	18	**San Luis Potosi.** 40 mi S of San Luis Potosi on Hwy 57. *Olsen 274.*
discoidea	18	**Chihuahua.** 15 mi E of Cuauhtemoc on Hwy 16. *Olsen 259.*
megacephala var. *megacephala*	18	**Hidalgo.** Road to El Chico, ca 4.5 mi N of Pachuca on Hwy 105. *Olsen 288.*
	18	**Hidalgo.** El Chico, road near La Ventura. *Olsen 289.*
mollissima	27	**Zacatecas.** Concepcion del Oro. *Olsen 297.*
	27	**Zacatecas.** 5 mi W of Concepcion del Oro on road to Mazapil. *Olsen 300.*

Table 2 (cont.)

TAXON	*n*	LOCALITY
		MEXICO:
mollissima	27	**Zacatecas.** Top of mountain on W side side of dirt road to Cadros; ca 16 mi N of Rosario. *Olsen 330.*
	27	**Zacatecas.** ca 2 mi E of Cedros on gravel road to Mazapil. *Olsen 331.*
	27	**Zacatecas.** 2 mi E of Mazapil on road to Concepcion del Oro. *Olsen 332.*
montagnifolia	18	**Puebla.** On Hwy 150d to Orizaba. *Olsen 245.*
	18	**Puebla.** ca 4 mi S of Esperanza on Mex 28 to Tehuacan. *Olsen 246.*
	18	**Puebla.** 4 mi S of Esperanza. *Olsen 247.*
	18	**Puebla.** 10 mi N of Tehuacan on Hwy 150. *Olsen 248.*
	18	**Puebla.** 16 mi N of Tehuacan on Hwy 190 to Puebla. *Olsen 249.*
		ECUADOR:
sodiroi	18	**Pichincha.** 6.5 km S of Quito on Pan American Hwy. *Olsen 435.*
	18	**Pichincha.** N of Machachi on Pan American Hwy. *Olsen 485.*
		MEXICO:
subcordata	ca 36	**Puebla.** 7 mi N of Esperanza on road to Ciudad Serdan. *Olsen 291.*
triloba	18	**Coahuila.** Hwy 4 at General Cepeda. *Olsen 306.*
	18	**Hidalgo.** ca 10 mi S of Ixmiquilpan. *Dillon 674.*

Table 2 (cont.)

TAXON	*n*	LOCALITY
		MEXICO:
triloba	18	**Hidalgo.** Junction of Hwy 45 and 85. *Olsen 285.*
	18	**Nuevo Leon.** 27 mi E of San Roberto Junction on Hwy 60 to Linares. *Olsen 340.*
	18	**Queretaro.** On Hwy 120, 29 mi N of Cadereyta. *Olsen 241.*
	18	**Queretaro.** 40 mi SW of Jalpan on Hwy 120. *Olsen 282.*
	18	**San Luis Potosi.** 11 mi S of Matehuala on Hwy 57. *Olsen 217.*
	18	**San Luis Potosi.** 18 mi W of San Luis Potosi on Hwy 49 toward Zacatecas. *Olsen 219.*
	18	**San Luis Potosi.** El Catorce. *Olsen 233.*
	18	**San Luis Potosi.** 15 mi S of Matehuala on Hwy 57. *Olsen 234.*
	18	**San Luis Potosi.** Along side of Hwy 57, 55 mi S of Matehuala. *Olsen 235.*
	18	**San Luis Potosi.** On Hwy 57 intersection with road to Guadalcazar. *Olsen 236.*
	18	**San Luis Potosi.** ca 20 mi N of San Luis Potosi on Hwy 57. *Olsen 237.*
	18	**San Luis Potosi.** ca 9 mi N of San Luis Potosi on Hwy 57. *Olsen 238.*
	18	**San Luis Potosi.** Just W of San Luis Potosi on Hwy 49. *Olsen 239.*
	18	**San Luis Potosi.** 6 mi E of San Luis Potosi on Hwy 70. *Olsen 240.*
	18	**San Luis Potosi.** 40 mi S of San Luis Potosi on Hwy 57. *Olsen 273.*

Table 2 (cont.)

TAXON	*n*	LOCALITY
		MEXICO:
triloba	18	**San Luis Potosi.** 4 mi E of San Luis Potosi on Hwy 70 toward Rio Verde. *Olsen 275.*
	18	**Zacatecas.** West end of Guadelupe on Hwy 49. *Olsen 220.*
	18	**Zacatecas.** 8 mi S of Fresnillo, on Hwy 45. *Olsen 250.*
	18	**Zacatecas.** 9 mi S of Fresnillo. *Olsen 263.*
	18	**Zacatecas.** 51 mi NE of Zacatecas on Hwy 54. *Olsen 294.*
	18	**Zacatecas.** 80 mi NE of Zacatecas on Hwy 54. *Olsen 295.*
	18	**Zacatecas.** 108 mi NE of Zacatecas on Hwy 54. *Olsen 296.*
	18	**Zacatecas.** Concepcion del Oro. *Olsen 298.*
	18	**Zacatecas.** 33 mi N of Fresnillo on Hwy 49. *Olsen 326.*
	18	**Zacatecas.** 15 mi N of junction Hwy 49 and 54 on road to Saltillo. *Olsen 328.*
	18	**Zacatecas.** 2 mi N of Rosario on dirt road to Cedros. *Olsen 329.*

the tetraploid level, hence the extant base of $x = 18$. It is also likely that ancestral polyploidy (hexaploidy and octoploidy) is responsible for the seemingly triploid *Z. mollissima* ($n = 27$) and the seemingly tetraploid *Z. subcordata* ($n = 36$), as is discussed below.

Zaluzania triloba, Z. augusta var. *augusta, Z. augusta* var. *rzedowskii, Z. montagnifolia, Z. megacephala* var. *megacephala, Z.*

sodiroi, and *Z. discoidea* all uniformly show $n = 18$ (although an $n = 16$, presumably erroneous, count has been reported for *Z. megacephala*) with the majority of the counts coming from the two most widespread taxa, *Z. triloba* and *Z. augusta* var. *augusta*. Meiosis is regular with consistently good pairing; in fact, no meiotic irregularity was seen in the configurations examined, including those of the polyploids.

Zaluzania mollissima ($n = 27$) is a robust shrub frequenting the rocky limestone slopes in the vicinity of Concepcion del Oro and Cedros, Zacatecas and, indeed, is known to occur only in this narrowly restricted bolson region. The occurrence of good bivalent pairing in this taxon is the strongest evidence in favor of an $x = 9$ base chromosome number for the genus. Assuming the base of $x = 9$, *Z. mollissima* would be a hexaploid. If $x = 18$ were the original base number, meiosis of the 54 chromosomes would have required autosyndesis of one set of 18 to give the observed 27II, or in other words, non-homologous chromosomes would be pairing during meiosis. If $x = 9$ were the ancestral condition, autosyndesis would reflect pairing of homologous chromosomes.

Morphologically, the two polyploids are nearest to diploid *Zaluzania augusta*. These three taxa are shrubby, have entire leaves with a soft woolly pubescence on the lower surface, and a pappus on the ray florets. *Zaluzania augusta* has the broadest geographic range of any species in the genus (Figure 2), and is the only ecological dominant (in terms of biomass) in the genus, occupying lower elevations and more mesic areas than either of the two polyploids. It seems likely that the morphological similarities exhibited by these three taxa would be best explained if they had all been derived from the same ancestral diploid stock, a *Z. augusta*-like ancestor. The polyploids, *Z. mollissima* and *Z. subcordata* therefore, would be interpreted as apoendemic taxa (Stebbins, 1971), narrowly restricted polyploid taxa, related to and possibly derived from a more widely distributed diploid.

In summation, the following points can be made from the cytological observations:

1. Although two of the 11 taxa remain to be counted, the extant base chromosome number for the genus is $x = 18$, with an $x = 9$ ancestral number strongly suggested.

2. The polyploid taxa are believed to be apoendemic entities.

3. The diploid *Zaluzania augusta* probably played a role in the production of the two polyploid taxa, although this conclusion is based only upon circumstantial evidence.

PALYNOLOGY

The primary reason for initiating a light microscope pollen survey in *Zaluzania* was to determine whether pollen size or aperture number correlates positively with ploidal level in the genus.

Table 3 summarizes the pollen data obtained for *Zaluzania.* The pollen grains are echinate and nearly spherical, varying in diameter from 22.5–30.0 microns. The spines are prominent and conical, ranging from 2.5–6.3 microns in length. All grains examined are uniformly three-apertured with long tapering colpi.

Grain size is not consistently correlated with ploidal level in the genus, and in fact is rather similar in all 11 taxa. The smallest grains are found in *Zaluzania augusta* var. *rzedowskii,* with *Z. pringlei, Z. augusta* var. *augusta* and *Z. subcordata* only slightly larger. The largest grains are found in *Z. sodiroi,* with *Z. discoidea, Z. triloba* and *Z. mollissima* only slightly smaller.

Polyploidy, especially if recent, often results in the increase in size of the individual cells, including pollen grains (Stebbins, 1950); however, the polyploid taxa *Z. mollissima* and *Z. subcordata* do not produce significantly larger grains than the diploid taxa. This suggests that the polyploids are of ancient origin, being now completely diploidized.

Of greater interest than just the size of the grains is the length of the spines. Spine length is to some extent correlated with pollination mechanism. Wodehouse (1945) states that there is a general trend for reduction in spine length, going from an entomophilous condition to an anemophilous condition, the entomophilous condition usually being considered primitive in the angiosperms (Cronquist, 1968). While all *Zaluzania* taxa are believed to be entomophilous, a trend from long spines to short spines does fit with other morphological data, suggesting that the very short spines (about 2.5 microns) found in the rayless, herbaceous taxon, *Z. discoidea* are derived, while the long spines (4.5–6.3 microns) found in the shrubby taxa, *Z. montagnifolia* and *Z. augusta* and the polyploids are more primitive.

Table 3

Measurements of acetolyzed Zaluzania pollen (in microns)

TAXON	POLAR DIAMETER	EQUATORIAL DIAMETER	SPINE LENGTH
Z. augusta			
var. *augusta*	24.5	22.0	4.7
var. *rzedowskii*	22.5	20.0	5.0
Z. discoidea	27.5	27.5	2.5
Z. megacephala			
var. *coahuilensis*	26.3	25.0	3.8
var. *megacephala*	25.1	23.0	5.0
Z. mollissima	27.5	26.3	5.0
Z. montagnifolia	25.3	22.1	6.3
Z. pringlei	22.7	22.1	3.8
Z. sodiroi	30.0	26.0	4.9
Z. subcordata	23.8	24.0	5.6
Z. triloba	27.5	26.9	4.9

There is no absolute difference in spine length between the herbaceous taxa and the shrubby taxa. In general, however, the pollen of the herbaceous members of the genus have shorter spines than pollen from the shrubs.

PHYLOGENY

In constructing a phylogenetic arrangement of taxa, it is always difficult to determine primitive versus advanced morphological states. This is certainly the case in *Zaluzania;* consequently, many of the assumptions are based on familiarity with the taxa and their distributions. To give a visual representation of my views, the Wagner Divergence Index (Wagner, 1961; Whiffen & Bierner, 1972) has been employed. Divergence index values are listed in Table 4.

Character	**Primitive**	**Advanced**
1. chromosome number	$n = 18$	$n = 27, 36$
2. flavonoids	glycosides	aglycones, absent
3. habit	shrub	herbaceous perennial, small trees
4. heads	many, small	few, large
5. leaf margins	entire, crenate	dentate, toothed
6. leaf pubescence	hirsute, pustulate	tomentose
7. pappus on the ray floret	present	absent
8. pollen	long spines	short spines
9. roots	no tubers	tubers

Figure 3 represents the tree derived from these characters. There is an obvious split between the shrubby taxa centering around *Zaluzania augusta* and *Z. montagnifolia* and the herbaceous perennial taxa centering around *Z. megacephala*. The shrubby taxa can be further subdivided into two groups. One is the coarsely pubescent, epappose group of three taxa, *Z. montagnifolia, Z. pringlei* and *Z. sodiroi*. The other is the densely soft-pubescent, larger headed group with a pappus on the ray florets, consisting of *Z. augusta, Z. mollissima,* and *Z. subcordata*.

Zaluzania augusta var. *augusta* is the extant taxon possessing the greatest number of primitive characters. This wide-ranging shrubby taxon occupies a region probably near the geographical center of dispersal for the genus. It is suggested that the ancestral *Zaluzania* originated in the region of the Mexican Plateau, occurring in submesic areas, habitats presently inhabited by *Z. augusta* var. *augusta*. This is supported by Rzedowski (1973), who states that the Mexican xerophytic flora (of which *Zaluzania* is today a part) derived from ancestors of neotropical or general tropical affinities and not from a southwestern United States flora pushed southward. The ancestral stock probably arose as a stabilized tetraploid derivative from an $x = 9$ line which also gave rise to *Viguiera*. With the uplifting of the Sierra Madre Oriental (Oligocene) and the subsequent increasing aridity of its western slopes (until Pleistocene, Maldonado-Koerdell, 1964), the environments suitable for *Zaluzania* moved to the west, causing ancestral *Zaluzania* to move with them. The peripheral

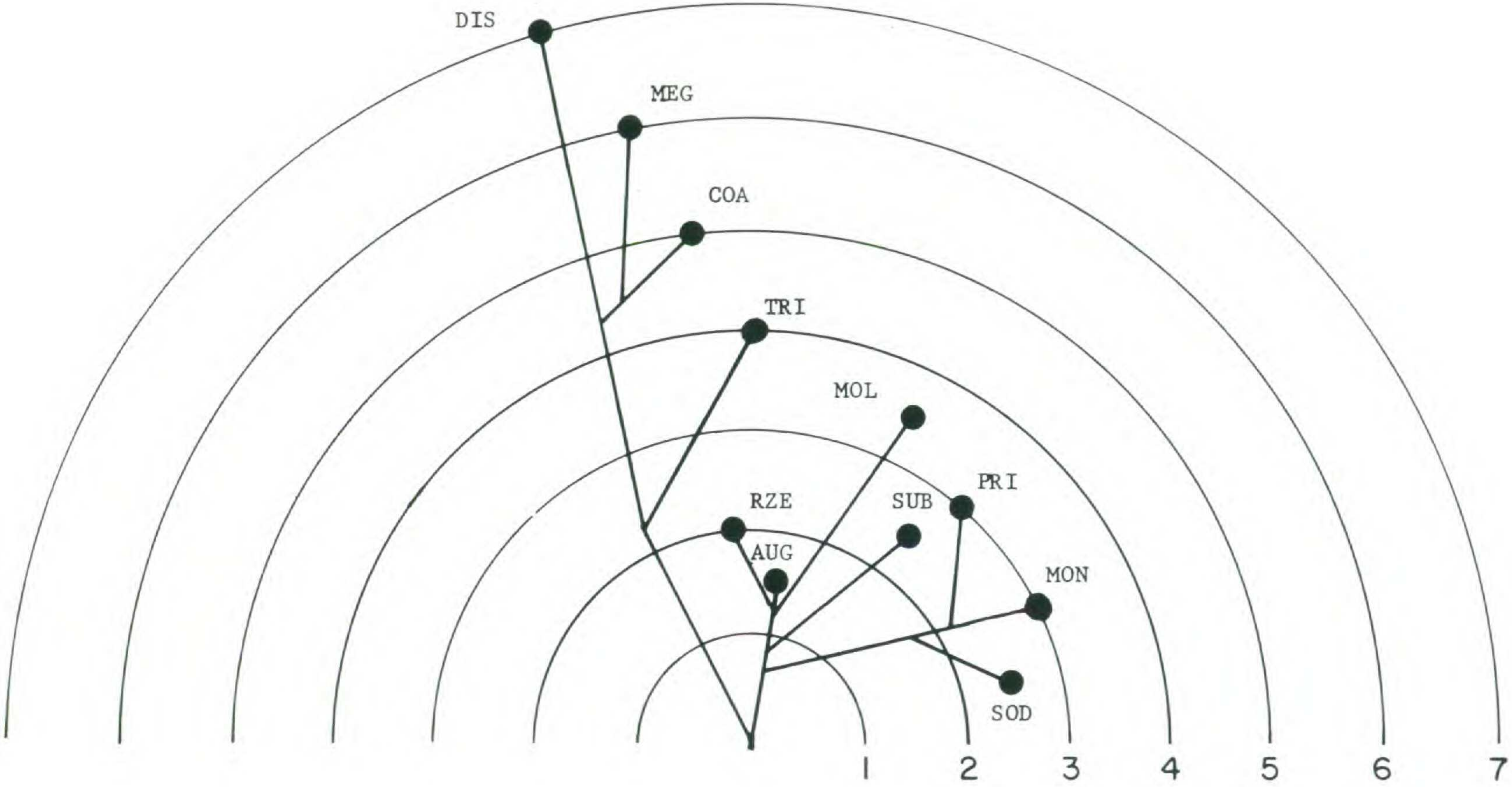

Figure 3. Relationships between *Zaluzania* taxa, indicated by divergence index values.

populations to the east which were pre-adapted to the arid conditions and presumably already isolated by polyploidy were left behind, where they are today represented by the apoendemic element, *Z. subcordata.*

Zaluzania montagnifolia inhabits the more mesic sites to the south of *Z. augusta.* This taxon is very woody in the south of its range, but this is viewed as a secondary adaptation and therefore a derived character (Carlquist, 1966 & 1976). This tendency is a common occurrence in the Asteraceae and reflects an adaptation of a more xeric element to mesic conditions (Carlquist, 1975). Radiation and evolution of this taxon probably gave rise to *Z. pringlei* to the south and west. It is also suggested that the Ecuadorian element, *Z. sodiroi,* could have arisen via chance introduction from *Z. montagnifolia* stock.

To the north and west, the Sierra Madre Occidental was being uplifted (Pliocene-Pleistocene, Axelrod, 1958; Johnson, 1968). This caused the movement of more arid conditions southward into Mexico. Presumably, evolution took place in response to this increasing aridity. The pre-adapted northern polyploid *Zaluzania mollissima,* already isolated chromosomally from *Z. augusta,* remained in the arid limestone hills to the north (Zacatecas) and is also best considered an apoendemic element.

The herbaceous perennials presumably arose from shrubby ancestors concurrently with the split of *Zaluzania augusta* var. *rzedowskii* from *Z. augusta* var. *augusta.* The similarity in flavonoid chemistry (Olsen, 1977b) of this variety and the herbaceous perennials suggests an origin from a common ancestor. These elements are all on the perimeter of the present range of *Z. augusta,* with *Z. megacephala* var. *megacephala* occupying very moist habitats in Tamaulipas and Hidalgo, *Z. megacephala* var. *coahuilensis* inhabiting the more xeric rocky hills of Coahuila; and *Z. augusta* var. *rzedowskii* occupying mesic areas in Zacatecas and Durango, south into Jalisco. *Zaluzania discoidea* to the north (in Durango and Chihuahua) inhabits disturbed areas along roadsides.

The widespread *Zaluzania triloba* occupies xeric sites in central and northern Mexico, but its relationships are uncertain. I have placed it in the herbaceous perennial line based on floral morphology; however, its sesquiterpene lactone chemistry (Yabuta et al., 1978) and flavonoid chemistry (Olsen, 1977b) are unique in the genus.

Table 4

Divergence index values for Zaluzania taxa

TAXON	1	2	3	4	5	6	7	8	9	TOTAL
Z. *augusta*										
var. *augusta*	0.0	0.5	0.0	0.0	0.0	1.0	0.0	0.0	0.0	1.5
var. *rzedowski*	—	0.0	0.0	0.5	0.0	1.0	0.5	0.0	0.0	2.0
Z. *subcordata*	1.0	0.5	0.0	0.0	0.0	1.0	0.0	0.0	0.0	2.5
Z. *sodiroi*	—	0.5	0.0	0.0	1.0	0.0	1.0	0.0	0.0	2.5
Z. *montagnifolia*	0.0	0.5	0.5	0.0	1.0	0.0	1.0	0.0	0.0	3.0
Z. *pringlei*	—	0.5	0.0	0.0	1.0	0.0	1.0	0.5	0.0	3.0
Z. *mollissima*	1.0	0.5	0.0	1.0	0.0	1.0	0.0	0.0	0.0	3.5
Z. *triloba*	0.0	1.0	1.0	0.0	1.0	0.0	1.0	0.0	0.0	4.0
Z. *megacephala*										
var. *coahuilensis*	—	0.0	1.0	1.0	0.5	0.5	1.0	0.0	1.0	5.0
var. *megacephala*	0.0	0.0	1.0	1.0	0.5	1.0	1.0	0.5	1.0	6.0
Z. *discoidea*	0.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	7.0

Zaluzania grayana is transferred here to *Viguiera*. The $n = 17$ chromosome number (Keil & Stuessy, 1975) and sterile ray florets are not known in *Zaluzania*. A list of some of the characters separating *Viguiera triloba* (Gray) Olsen (*Z. grayana*) from *Zaluzania* is presented below.

Zaluzania	**Viguiera triloba**
$n = 18, 27, 36$	$n = 17$
rays fertile; ligules short (except in *Z. mollissima*) and not showy	rays sterile; ligules long and showy
leaves not papery textured; pubescence hirsute to woolly	leaves thin and papery; pubescence sparse
involucre not spreading; inner series becoming scarious (at least along the margins)	involucre spreading; inner series strictly herbaceous

It has been suggested (H. Robinson, pers. comm.) that *Viguiera triloba* does indeed belong in *Zaluzania* because of the unique expansion of the disc corolla in these taxa to form a cap over the achene. Further examination of this character, however, has shown that the expansion referred to is also found in *Viguiera*, although not to the extent seen in *Zaluzania*. Several taxa in *Viguiera* series *Maculatae* and *Grammatoglossae* have the fleshy cap over the achene. Since this one character is not a consistent distinguishing feature, *V. triloba* is believed to belong in *Viguiera*, where the characters noted above would indicate its affinities to be.

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TAXONOMIC TREATMENT

Zaluzania Persoon, Syn. Plant. **2:** 473. 1807.

Ferdinanda Lag., Gen. Sp. Nov. Pl. **31.** 1816.
Chrysophania Kunth ex Less., Syn. Gen. Comp. **224.** 1832.

Herbaceous or shrubby perennials to 4m in height. Stems glabrous below to tomentose above, 1 to many from a woody caudex (roots in herbaceous perennials usually with fleshy tubers). Leaves entire to tripartite; blades cordate, ovate, or lanceolate-elliptic in outline, sessile or attenuate if petiole present, hirsute to lanate below, pustulate to lanate above, hairs simple. Inflorescence corymbose, peduncles to 10 cm in length. Heads usually radiate (one species strictly discoid), 1.0–3.1 cm in diameter, including the rays. Involucre 2–3 seriate, the bracts herbaceous, linear-lanceolate, pubescent, the inner series glabrate and chartaceous. Receptacle conical. Chaff present, the pales oblanceolate in outline, trifid at the apex, enclosing the disc florets. Ray florets, when present, 4–10, pistillate and fertile, yellow (white in one species); style branches linear, enclosed in the tube or well exserted. Disc florets 40–100, hermaphroditic and fertile, yellow (white in one species); base of the corolla tube usually expanded to form a cap over the achene; style branches short, flat, stigmatic lines indistinct, appendage acute. Anthers sagittate at base; pollen echinate, polar diameter 22.5–30.0 microns, equatorial diameter 20.0–27.5 microns, spines 2.5–6.3 microns in length. Ray achenes 3-angled in cross section, black, glabrous or pubescent along the angles; pappus of 2–4 scales, or absent. Disc achenes black, 4-angled in cross section, glabrous; pappus absent. Base chromosome number $x = 18$.

TYPE SPECIES: *Zaluzania triloba* (Ort.) Pers.

KEY TO THE SPECIES

- a. Herbaceous perennials.............. b.
  - b. Leaves tripartite, sometimes more highly dissected; pubescence hirsute. .... 1. *Z. triloba*
  - b. Leaves undivided; pubescence tomentose to lanate. .... c.
    - c. Heads discoid. .... 2. *Z.discoidea*
    - c. Heads radiate. .... 3. *Z. megacephala*
- a. Shrubs.............. d.
  - d. Leaf margins entire; ray florets with a pappus of 2–4 awns.......... e.
    - e. Heads more than 2 cm wide (including the rays)... 4. *Z. mollissima*
    - e. Heads less than 1.5 cm wide (including the rays).............. f.
      - f. Leaves cordiform; ligules less than 5 mm in length; disc corolla tube expanded to cap the achene. ....5. *Z. subcordata*
      - f. Leaves ovate-lanceolate to ovate; ligules more than 5 mm in length; disc corolla tube not inflated to cap the achene. ..6. *Z. augusta*
  - d. Leaf margins serrate; ray florets epappose.............. g.
    - g. Heads (usually discoid) white; ray florets (if present) white. .... 7. *Z. pringlei*
    - g. Heads radiate; yellow. .... h.
      - h. Pubescence of upper leaf surface pustulate; throat of the disc and ray corollas weakly pubescent; plants of Mexico. .... 8. *Z. montagnifolia*
      - h. Pubescence of upper leaf surface not pustulate; throat of the disc and ray corollas glabrous; plants of Ecuador..... 9. *Z. sodiroi*

1. **Zaluzania triloba** (Ort.) Pers., Syn. Plant. **2:** 473. 1807.

Anthemis triloba Ort., Desc. Pl. Rar. **72.** 1798. TYPE: MA. (Isotype, L; Photograph of Isotype, MO!).

Athemis sinuata LaLlave & Lexarza, Nov. Veg. Desc. **1:** 26. 1825. Type not designated; described from the vicinity of Los Remedios and San Angel, Mexico.

Acmella trilobata Spreng., Linn. Syst. Veg. **3:** 591. 1826. Based upon *Anthemis triloba* Ort.

Aiolotheca parthenioides DC., Prodr. **5:** 508. 1836. TYPE: G-DC. *Berlandier 1341.* MEXICO: San Luis Potosi. Hacienda de la Encarnacion. Dec., 1827. (Phototypes, F!, LL!; Isotype, GH!).

Zaluzania robinsonii W. M. Sharp, Ann. Missouri Bot. Gard. **22:** 105. 1935. TYPE: MO! *Lloyd 124.* MEXICO: Zacatecas. Hacienda de Cedros. Aug., 1907. (Isotypes, LL!, UC!).

Zaluzania parthenioides (DC.) Rzedowski, Brittonia **20:** 166. 1968.

Herbaceous perennials to 1 m in height. Stems 1 to several from a woody caudex, usually striate; puberulent below to hirsute above. Roots without fleshy tubers. Leaves tripartite, becoming more highly dissected. Upper leaves 1.8–3.0 cm long, 1.4–2.1 cm wide; lower leaves 6.3–7.5 cm long, 4.2–5.5 cm wide; pubescence of the upper surface strigose, lower surface strigose to hirsute; petioles up to 1.5 cm in length. Peduncles 0.5–1.2 cm long, hirsute to tomentose. Heads 0.8–1.4 cm in diameter (including the rays). Involucre 2-seriate, the bracts lanceolate, outer series 2.5–3.0 mm long, 0.7–1.1 mm wide, inner series becoming trifid, equal in length, but broader. Pales oblanceolate in outline, trifid. Ray florets 8–10, ligules yellow, 3-lobed, 3.1–4.2 mm long, 2.5–3.5 mm wide; throat pubescent, styles well exserted from the tube. Disc florets about 75, yellow, corolla 1.8–2.2 mm long, 1.3–1.6 mm wide; throat minutely pubescent. Ray achenes hairy along the angles and the summit, 1.0–2.1 mm long, 0.3–0.6 mm wide; pappus absent. Disc achenes 1.0–1.3 mm long, 0.5–0.6 mm wide. (Figure 4).

REPRESENTATIVE SPECIMENS. MEXICO. **Aguascalientes:** shrub covered, nearly treeless mountainsides about 20 km E of Rincon de Romos, road to Asientos, between Cerro Altamira and Cerro de San Juan, *McVaugh 23744*, (MICH); Ladera N del Cerro San Juan, 5 km al E de Tepezala, *Rzedowski 25008* (MICH). **Coahuila:** 5 mi S of Saltillo, *Barkley 16037* (F, LL); In low places along the roadside in *Larrea* association, 6 mi N of Saltillo, *Cronquist 9840* (GH, LL, MICH, NY); Road from Saltillo S to Concepcion del Oro, Carneros Pass, *Johnston 7285* (GH); 1 mi N of Carneros, *Johnston & Graham 4189c* (MICH); La Encantada, 9 mi W of Saltillo, *Mears 32410* (LL); Highway 4 at General Cepaeda, *Olsen 306* (LL); Near Saltillo, *Palmer 360* (F, GH, MO, NY, UC, US); Parras, *Palmer 435* (GH, MO, NY, UC, US); Carneros Pass, *Pringle 2402* (F, GH, LL, MICH, MO, NY, UC, US); Carneros Pass, 21 mi S of Saltillo, *Shreve 8549* (ARIZ, MICH, US). **Federal District:** Vicinity of Rancho del Flores near San Pablo, 15 mi S of Mexico City, *Happ 294* (MO); Santa Maria Astahuacan, delegacion de Ixtapalapa, *Rzedowski 27867* (MICH). **Guanajuato:** San Luis de la Paz, *Kenoyer 2325* (GH). **Hidalgo:** 17 mi W of Tulancingo at village called Jalapilla, along Hwy, *Bierner & Turner 124* (LL); ca 10 mi SE of Ixmiquilpan, *Dillon 674* (LL); Pachuca, *Fisher 35245* (ARIZ, F, LL, MO, NY, US); Zimapan, *Hartweg 329* (NY); Junction Hwy 45 and 85, *Olsen 285* (LL); Sierra de Pachuca, *Pringle 9481* (F, GH, MEXU, MO, US); Calcareous mesas near Zontecomate Station, *Pringle 13093* (ARIZ, F, GH, LL, MICH, US); Near Tula, *Rose 8325* (GH, US); Hill-slopes behind Hacienda Tetlapayac, 12 km E of Apan, *West FF-8* (MICH). **Mexico:** Las Cruces, Hwy to Toluca, *Matuda 19227* (MEXU). **Nuevo Leon:** Near Casablanca, *Barkley 16016* (F, LL); 27 mi S of San Roberto Junction along Hwy 56, *Bierner & Turner 98* (LL, NY). **Oaxaca:** Al NE de Cuicatlan, *Miranda 4694* (MEXU). **Puebla:** 37 mi SE of Tehuacan and 2.5 mi N of Teotitlan, *Cronquist & Sousa 10384* (MEXU); Along rt 150, ca 20 mi NW of Tehuacan, *King 2639* (LL, MICH, UC, US). **Queretaro:** Del Ciervo of San Juan, *Altamirano s.n.*, 27 Aug 1905 (US); On Hwy 120, 29 mi N of Cadereyta, *Olsen 241* (LL); 40 mi SW of Jalpan on Hwy 120, *Olsen 282* (LL). **San Luis Potosi:** Matehuala a Rio Blanco, *Berlandier 3170* (MO); San Luis Potosi, *Fisher 136* (GH, US); 3 mi W of Ciudad del Maiz, *Johnston & Graham 4442* (LL, MEXU); 11 mi S of Matehuala on Hwy 57, *Olsen 217* (LL); 18 mi S of junction at

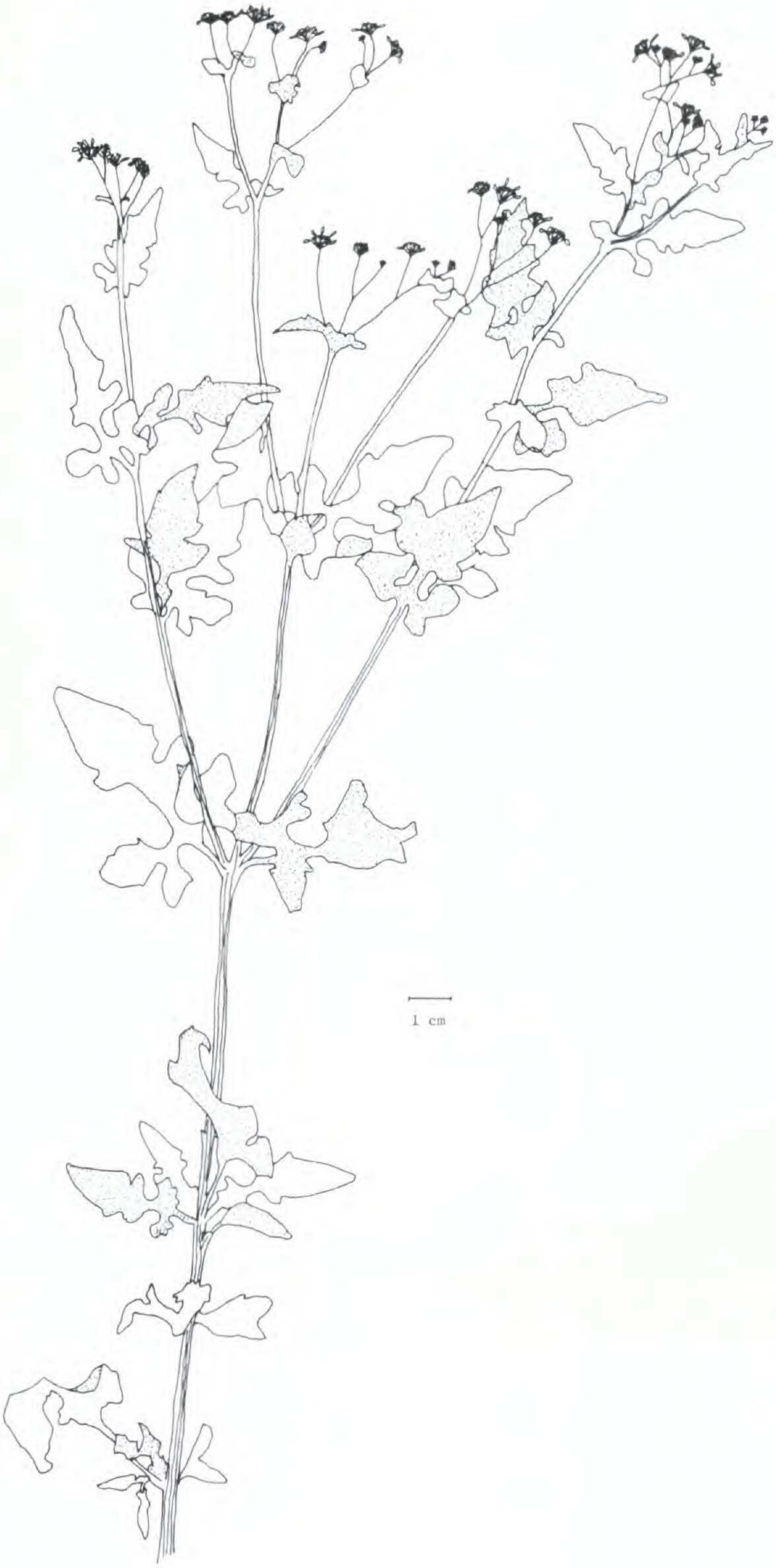

Figure 4. *Zaluzania triloba,* habit tracing.

Huizache on Hwy 57, 68 mi S of Matehuala, *Olsen 218* (LL); 18 mi W of San Luis Potosi on Hwy 49 toward Zacatecas, *Olsen 219* (LL); El Catorce, *Olsen 233* (LL); 40 mi S of San Luis Potosi on Hwy 57, *Olsen 273* (LL); 4 mi E of San Luis Potosi on Hwy 70 toward Rio Verde, *Olsen 275* (LL); Vanegas, *Pennell 17510* (GH, MEXU, US); Los Charcos, *Pringle 4026* (MICH); Along arroyo running through shrubs 25 mi NE of San Luis Potosi, *Waterfall 15707* (US). **Tamaulipas:** Near town of Miquihauana, *Stanford, Retherford & Northcraft 820* (ARIZ, GH, MO, NY, UC). **Vera Cruz:** Orizaba, *Botteri 843* (US); Justo Sierra, Municipio de Perote, *Ventura 4007* (LL, MICH). **Zacatecas:** In open thorn scrub communities dominated by *Acacia* and tree *Opuntias,* 20 mi SE of Zacatecas, *Cronquist 10533* (MEXU, MICH, NY, US); 34 air mi WNW of Concepcion del Oro, 9.2 mi W of Cedros, *Henrickson 6344b* (LL); West end of Guadalupe, Hwy 49, *Olsen 220* (LL); 8 mi S of Fresnillo on Hwy 45, *Olsen 250* (LL); 51 mi NE of Zacatecas on Hwy 54, *Olsen 294* (LL); Concepcion del Oro, *Olsen 298* (LL); Cactus savanna 21 mi S of Santa Maria de Manon, *Shreve 8627* (ARIZ, MICH, US); about 70 mi N of Zacatecas on road to Saltillo, *Strother 1116* (UC).

Zaluzania triloba (commonly called 'hierba amargosa') occurs at altitudes of 1500–2800 m. It is sympatric with two other *Zaluzania* species, *Z. augusta* and *Z. mollissima,* and is most commonly found in association with *Larrea tridentata* and species of *Acacia, Flourensia, Jatropha, Opuntia, Verbesina* and *Viguiera.*

Zaluzania triloba has been treated as two species by various authors, but close inspection of the morphological variation in the group does not support this splitting. Sharp (1935) separated *Z. robinsonii* from *Z. triloba* on the basis of pubescence, leaf dissection, head diameter, and stem striation. Rzedowski (1968) accepted Sharp's species, but noted it to be synonymous with the earlier *Aiolotheca parthenioides,* hence the name *Z. parthenioides* (DC.) Rzedowski.

Based upon examination of the material concerned and extensive field work on *Zaluzania triloba* from throughout its range, I conclude that the characters used to separate these taxa intergrade completely. Indeed, within the same population, plants found growing in the sun usually have the characters attributable to *Z. triloba,* while plants found growing in the shade have the characters attributable to *Z. parthenioides.* Both growth forms are diploid and both are found throughout the range of the taxon.

2. **Zaluzania discoidea** Gray, Proc. Amer. Acad. **21:** 388. 1886. TYPE: GH! *Pringle 309.* MEXICO: **Chihuahua.** Rocky hills near Chihuahua, 19 Oct 1885 (Isotypes: F!, LL!, NY!, US!).

Herbaceous perennials to 2 m in height. Stems single, arising from a woody caudex, unbranched until the inflorescence, pubescent along the entire length. Roots with fleshy tubers. Leaves cordate to ovate, the margins serrate to undulate, glandular, upper leaves 1.6–5.8 cm long, 0.6–2.5 cm wide; lower leaves 7.0–15.7 cm long, 6.3–15.3 cm wide; pubescence of the upper surface strigose, lower surface tomentose; petioles 0.2–2.2 cm in length. Peduncles 0.3–2.4 cm in length, densely pubescent. Heads discoid, 0.3–1.0 cm in diameter. Involucre 2–3 seriate, the bracts elliptical, outer series 3.9–4.2 mm long, 1.8–2.2 mm wide; inner series slightly longer and narrower. Pales oblanceolate, trifid, 3.4–3.6 mm long, 1.0–1.2 mm wide. Disc florets ca 75, corolla yellow, 2.5–3.6 mm long, 1.5–2.0 mm wide, throat pubescent. Achenes 1.8–2.0 mm long, 0.7–0.9 mm wide. (Figure 5.)

REPRESENTATIVE SPECIMENS. MEXICO. **Chihuahua:** Majalca, *LeSueur Mex-143* (ARIZ, LL); 63 mi W of Parral on road to El Vergel, *Correll & Gentry 22871* (LL); Parral and vicinity, Rio San Juan Valley along road from Parral, *Gentry, Correll, & Arguelles 18088* (US); 15 mi E of Cuauhtemoc on Hwy 16, *Olsen 259* (LL); Mountains near Chihuahua, *Pringle 1110* (LL, MEXU, MO, NY, UC). **Durango:** El Oro to Guanecevi, *Nelson 4727* (US); along road between Cerro Prieto and La Providencia, *Nelson 4970* (NY, US).

Zaluzania discoidea occurs on rocky clay soils among rolling hills at elevations of 1900–2200 m. It is most commonly found in disturbed areas along fenced fields, but also occurs in open wooded areas and grasslands. Taxa commonly found in association with *Z. discoidea* include species of *Machaeranthera, Quercus* and *Zinnia,* as well as many grasses.

Gray (1886) believed *Zaluzania discoidea* to be closely related to *Z. augusta* and *Z. mollissima.* It does not appear, however, to be very close to the latter, a shrubby taxon with long ray florets and lanceolate leaves. The ovate, densely pubescent leaves, erect unbranched habit and compact inflorescence of *Z. discoidea* do suggest a close relationship with *Z. augusta.* In any event, *Z. discoidea* is clearly related to the other herbaceous perennial taxa, these forming a closely knit phyletic group. On total characters, it is most closely related to *Z. megacephala,* the latter differing primarily in being radiate.

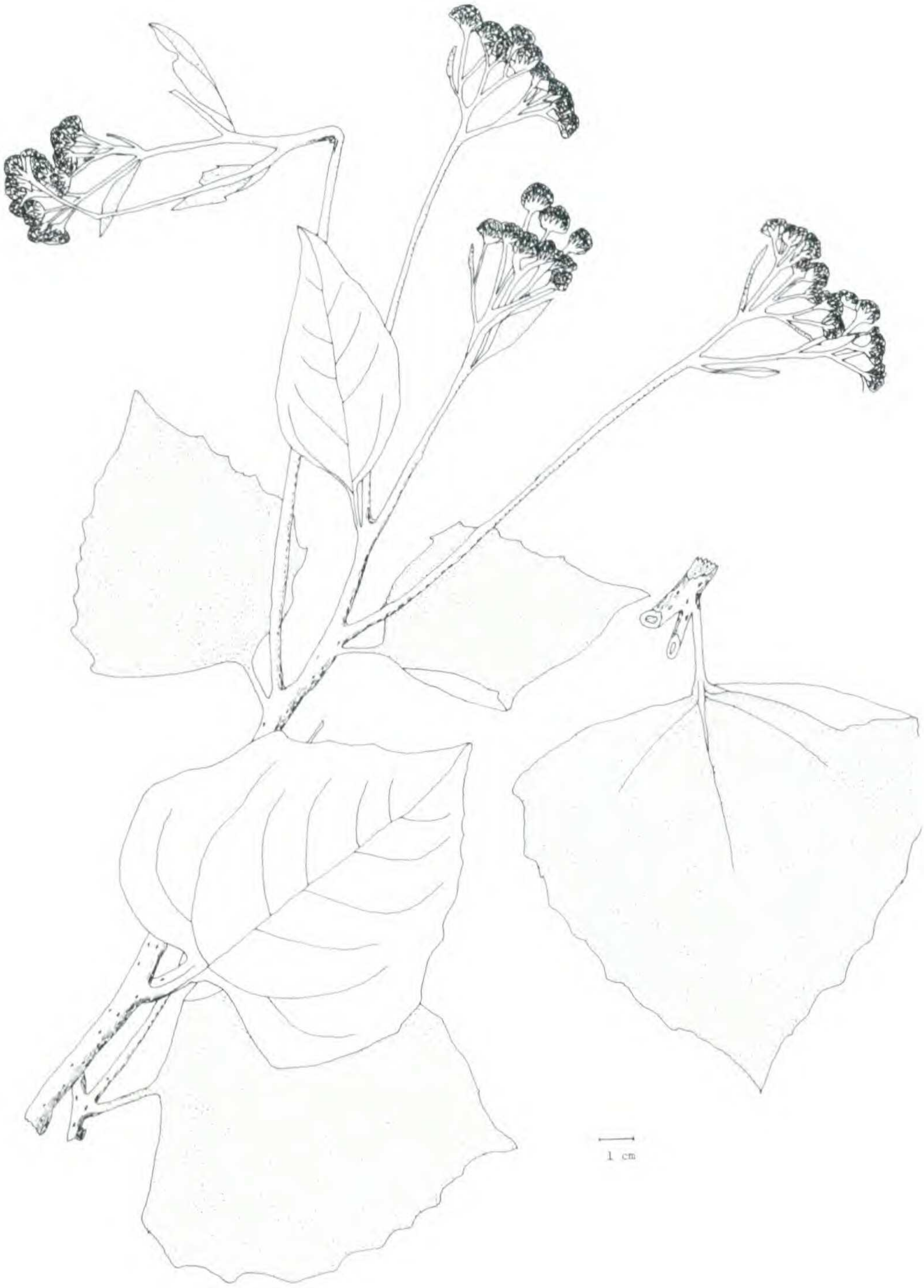

Figure 5. *Zaluzania discoidea*, habit tracing.

3. **Zaluzania megacephala** Sch.-Bip., Flora **44:** 563. 1861. (Typification and synonymy cited under varietal names.)

Herbaceous perennials to 1.5 m in height. Stems 1, or less commonly 2, from a woody caudex, unbranched until the inflorescence, reddish in color, glabrous at base to densely pubescent at the inflorescence. Roots with fleshy tubers. Leaves lanceolate-elliptic to ovate, the margins glandular-serrulate or serrate; upper leaves 3.5–7.5 cm long, 1.0–4.7 cm wide; lower leaves 6.6–13.0 cm long, 3.0–8.0 cm wide; pubescence of the upper surface strigose to tomentose, lower surface densely tomentose. Petioles 0.5 cm long or less. Peduncles 1.0–5.0 cm long, pubescent. Heads 1.4–2.7 cm in diameter (including the rays). Involucre 2–3 seriate, the bracts linear lanceolate in the outer series, apex truncate in the inner series; outer series 3.5–6.7 mm long, 0.7–2.5 mm wide, inner series shorter and broader. Pales 3.7–4.2 mm long, 1.2–2.5 mm wide. Ray florets 8–10, yellow, 4.2–14.0 mm long, 2.4–6.0 mm wide; throat pubescent with a few ascending hairs; style branches very short, not extending from the tube. Disc florets ca 75, yellow; corolla 1.6–3.4 mm long, 0.7–2.4 mm wide; throat sparsely pubescent. Ray achenes glabrous to sparsely pubescent, 0.8–2.6 mm long, 0.4–1.0 mm wide; pappus absent. Disc achenes 1.5–3.1 mm long, 0.4–1.0 mm wide.

KEY TO THE VARIETIES

a. Leaves ovate (rarely ovate-elliptic); margins serrulate; upper surface usually tomentose. .... 3a. var. *megacephala* (Figure 6)

a. Leaves lanceolate-elliptic (rarely ovate-elliptic); margins serrate; upper surface strigose. .... 3b. var. *coahuilensis* (Figure 7)

3a. **Zaluzania megacephala** Sch.-Bip. var. **megacephala** (Figure 6).

Zaluzania megacephala Sch.-Bip., Flora **44:** 563. 1861. TYPE: B. *Ehrenberg 462.* MEXICO: **Hidalgo:** Real del Monte. w/o date. (Phototype, GH!).

Zaluzania cinerascens Sch.-Bip., Flora **47:** 219. 1864. TYPE: B. *Ehrenberg 346.* MEXICO: **Hidalgo:** Mineral del Monte. w/o date. (Isotype, GH!; Phototype, GH!).

Zaluzania coulteri Hemsl., Diagn. Sp. Nov. **33.** 1879. TYPE: K. *Coulter 350.* MEXICO: **Hidalgo.** Real del Monte. w/o date. (Isotype, GH!).

REPRESENTATIVE SPECIMENS. MEXICO. **Federal District:** Sierra de Guadalupe, *Balls 5602* (US). **Hidalgo:** Sierra de Pachuca, ridge ca 2 km S of Real del Monte, *Beaman 2743* (GH); El Chico, *Lyonnet 387* (GH, MO, NY, US); Real del Monte, *Matuda 21659* (NY); Camino de Chico, *Matuda 25630* (MEXU, NY); Zimapan, *Moore & Wood*

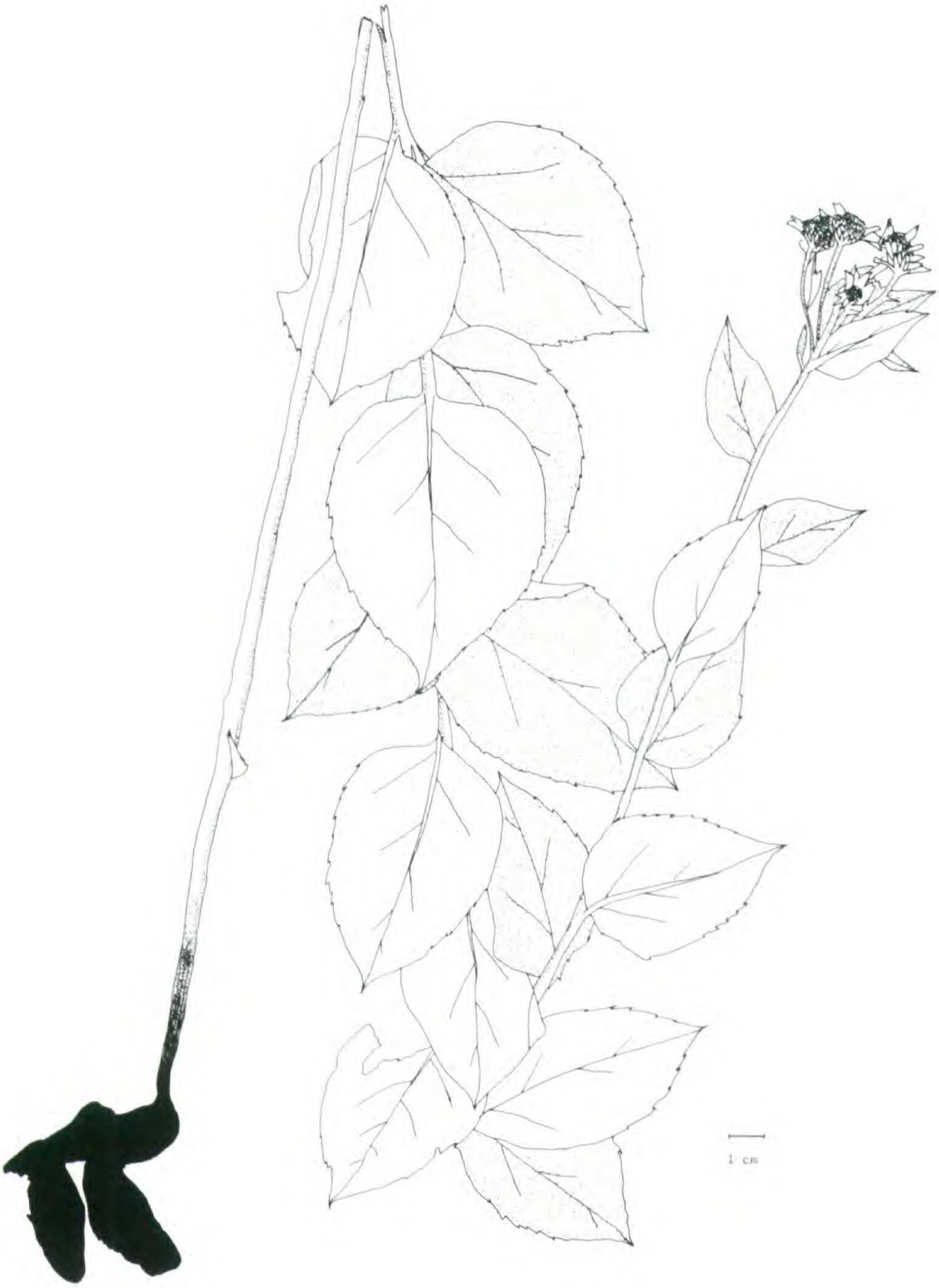

Figure 6. *Zaluzania megacephala* var. *megacephala*, habit tracing.

44817 (NY); Road to el Chico, ca 4.5 mi N of Pachuca on Hwy 105, *Olsen 288* (LL); El Chico, road near La Ventura, *Olsen 289* (LL); Bosque de Encinos, *Paray 3218* (MEXU); Sierra de Pachuca, *Pringle 6956* (F, GH, MICH, MO, NY, UC, US), *Pringle 9997* (F, GH, MO, NY), *Pringle 13784* (ARIZ, GH, LL, MICH, US); Cerro de las Ventanas, 6 km al N de Pachuca, *Rzedowski 23025* (LL, MICH); El Bordo, 4 km N of Pachuca, *Rzedowski 24299* (F, LL, MICH); 3 km E del Cerro de las Ventanas, *Rzedowski 26824* (ARIZ, LL, MICH, US); Real del Monte, above Pachuca, *Sharp 44608* (NY); Oak forests near Real del Monte, above Pachuca, *Sharp 441086* (NY). **Nuevo Leon:** Cerro Potosi, east slope, *McGregor 361* (NY); E side of Cerro Linadero, *Meyer & Rogers 2905* (GH, MO, US); Cieneguillas to Puerto Santa Ana, about 15 mi SW of Galeana, *Mueller 909* (F, GH, LL, MICH); Cieneguillas, Pablillo, SE of Galeana, *Pennell 17094* (GH). **Queretaro:** 12 km al SW de Pinal de Amoles, sobre la carretera a Vizarron, *Rzedowski 27833* (F, MICH, NY). **Tamaulipas:** 4 km W of Miquihauana in canyon with luxuriant vegetation, *Stanford, Retherford, & Northcraft 673* (ARIZ, GH, MO, NY); 3 mi N of Miquihauana in pine forest, *Stanford, Lauber, & Taylor 2422A* (NY, US), *Stanford, Lauber, & Taylor 2434* (LL, NY, US).

This taxon has long gone under the name *Zaluzania cinerascens.* Schultz-Bipontinus gave only a very sketchy description of *Z. megacephala,* an Ehrenberg collection from Hidalgo. For some reason, he described a second species, *Z. cinerascens,* from other collections at the same locality (made by the same collector). Unfortunately, neither Robinson and Greenman (1899) nor Sharp (1935), in their revisionary studies of the genus, examined the types concerned and consequently did not recognize that the two names applied to the same taxon. Instead, they applied *Z. megacephala* to those populations around Saltillo, which as noted below are undescribed, and applied *Z. cinerascens* to those populations from Hidalgo, typified by *Z. megacephala,* a name which must be applied to the Hidalgo populations if these are to be recognized as distinct.

While the two recognized population groups are morphologically distinct and occupy different geographic regions, the characters distinguishing them are relatively trivial compared with those distinguishing other specific taxa; consequently, the populations concerned are recognized as only varietally distinct.

Variety *megacephala* is a high montane element, occurring primarily in the damp, pine-oak forests of eastern Mexico, at elevations above 3100 m.

3b. **Zaluzania megacephala** Sch.-Bip. var. **coahuilensis** Olsen, *var. nov.* TYPE: LL! *Pringle 10076.* Mountains near General Cepeda, 6500 ft, 7 Oct 1905 (Isotypes: F!, GH!, MO!, NY!, UC!, US!).

A varietate typica foliis lanceolato-ellipticis (raro ovato-ellipticis) margine serratis supra strigosis differt. (Figure 7).

REPRESENTATIVE SPECIMENS. MEXICO. **Coahuila:** La Casita, *Kenoyer & Crum 3016* (MICH); Cañon and elevated portions of Sierra Madre, 14 leagues S of Saltillo, *Palmer 734* (F, GH, NY, US); High summits near Carneros Pass, *Pringle 2398* (GH, MEXU, MICH, MO, NY, UC, US). **Durango:** El Salto (Aserrederos), *Pennell 18521* (NY, US). **Nuevo Leon:** Upper W slope of la Sierra de la Cebolla, Municipio de Rayonnes, *Mueller 2908* (GH, LL).

This taxon is also found in grassy pine-oak forests, but the habitats are typically lower and drier than those typifying *Zaluzania megacephala* var. *megacephala.* One collection, *Pennell 18521,* from Durango, appears to be far out of range for this taxon. Its location suggests *Z. augusta* var. *rzedowskii,* but leaf pubescence and epappose ray florets show it to be *Z. megacephala* var. *coahuilensis.*

Zaluzania megacephala is most closely related to *Z. discoidea.* Both are erect herbaceous perennials with compact, corymbose inflorescences. They differ primarily in characters of leaf pubescence, and *Z. discoidea* is obviously eradiate.

4. **Zaluzania mollissima** Gray, Proc. Amer. Acad. **15:** 35. 1880. TYPE: GH! *Parry & Palmer 445.* MEXICO. San Luis Potosi: Vicinity of San Luis Potosi, Aug 1878 (Isotypes: F!, MO!, NY!, US!).

Perennial shrubs to 2.5 m in height. Stems glabrous at base to tomentose above. Roots without fleshy tubers. Leaves lanceolate-elliptic, tending to become three lobed, margins entire; upper leaves 1.6–2.8 cm long, 0.6–0.8 cm wide; lower leaves 4.2–7.5 cm long, 1.4–2.0 cm wide; pubescence of the upper surface tomentose, lower surface lanate. Petioles less than 1.0 cm in length, pubescent. Heads 2.2–3.5 cm in diameter (including the rays). Involucre 3-serriate, the bracts lanceolate; outer series 3.3–3.6 mm long, 1.0–1.3 mm wide, inner series slightly longer. Pales oblanceolate, weakly trifid, 3.8–4.2 mm long, 1.3–1.6 mm wide. Ray florets 8–10, ligules yellow, 3-lobed, 10.7–11.4 mm long, 3.8–4.2 mm wide, throat pubescent, styles well exserted from the tube. Disc florets ca 50, corolla yellow, 2.3–2.7 mm long, 1.8–2.4 mm wide; throat glabrous. Ray achenes glabrous, 1.9–2.3 mm long, 0.8–1.1 mm wide; pappus of 2 scales or absent. Disc achenes 2.4–2.8 mm long, 0.6–0.9 mm wide. (Figure 8).

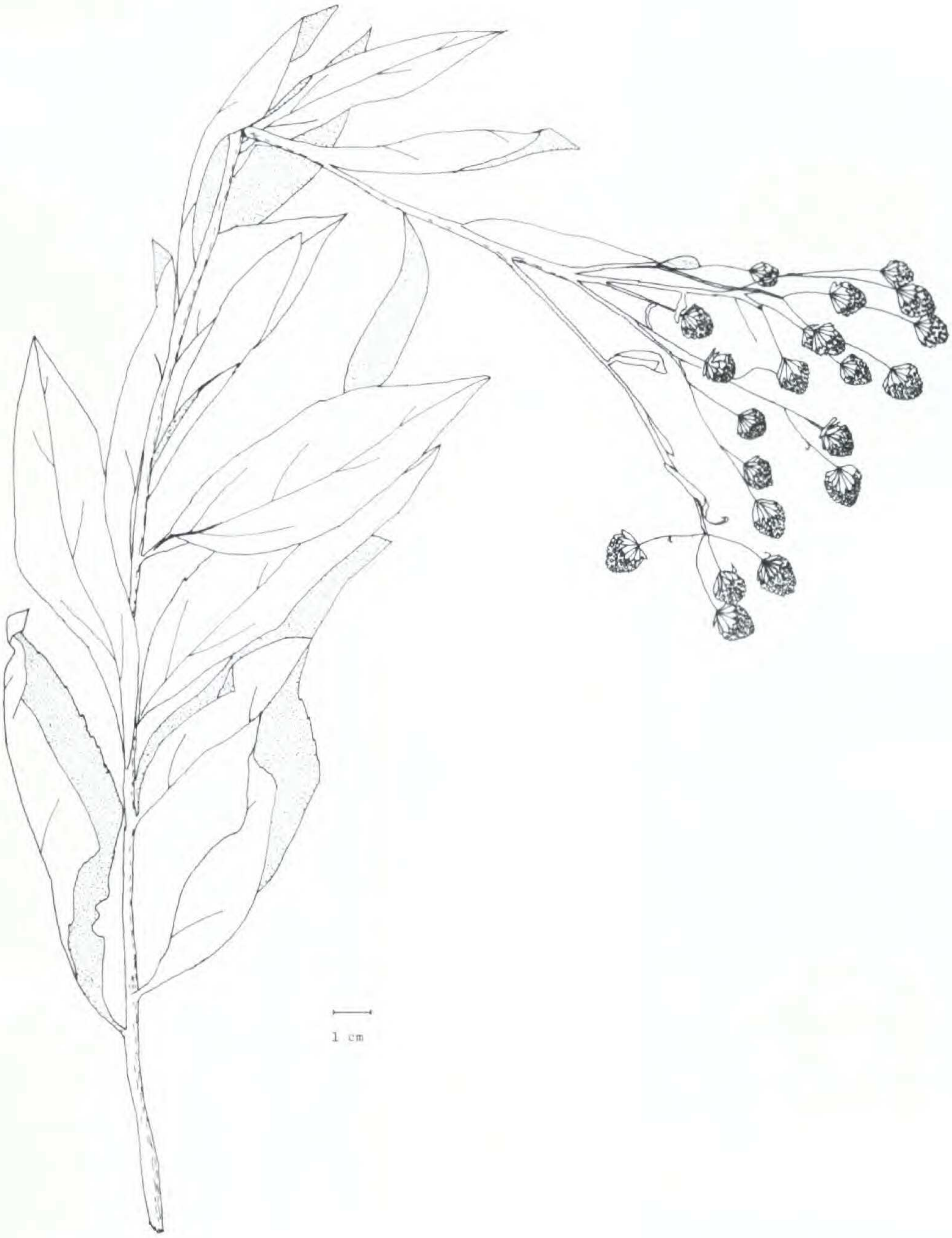

Figure 7. *Zaluzania megacephala* var. *coahuilensis*, habit tracing.

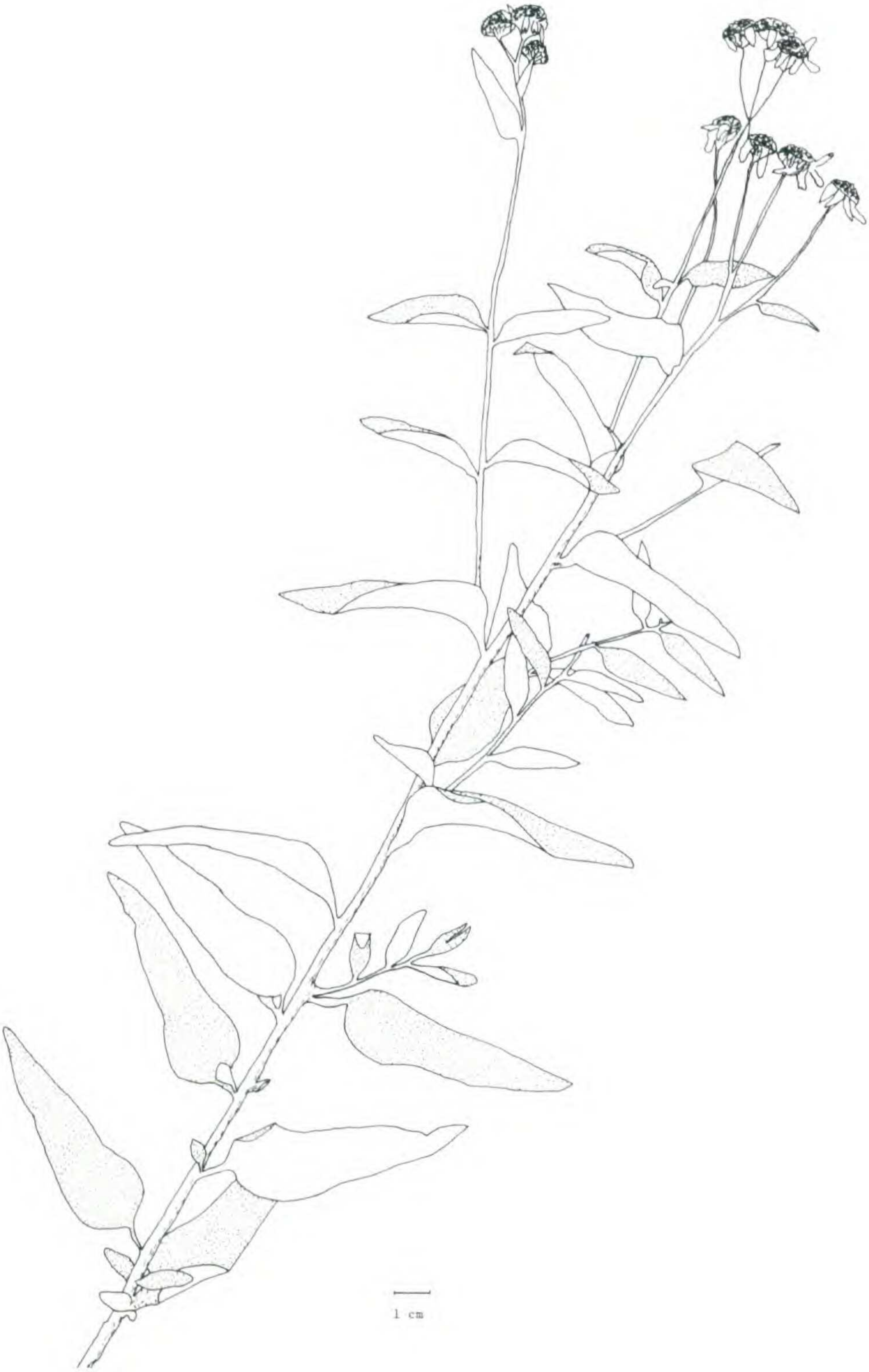

Figure 8. *Zaluzania mollissima,* habit tracing.

Representative Specimens. MEXICO. **Coahuila:** In valley 15 km W of Concepcion del Oro, just within Coahuila border, *Stanford, Retherford, & Northcraft 515a* (ARIZ, GH, MO, NY, UC). **San Luis Potosi:** Penasco, *Rzedowski 3442* (F, US); San Miguel, *Schaffner 767(342)* (MICH, NY, US). **Zacatecas:** 1 mi W of Concepcion del Oro along road to the main mine, *Henrickson 6252* (LL); 13.1 road miles W of Concepcion del Oro on road to Mazapil, *Henrickson 6293* (LL); ca 12 air miles NE of Estacion Camacho, 2 mi W of Pico de Teyra, *Henrickson 13398* (LL); 5 mi S of Majoma, *Johnston 7392* (GH, US); 2.5 km E of Mazapil on Hwy. Concepcion del Oro, *Johnston, Wendt, & Chiang 11544* (LL); In relatively wet places, vicinity of Cedros, *Kirkwood s.n.*, May 1908 (F); Hills near Cedros, *Lloyd 32* (GH); Zacatecas, *Lloyd 129* (LL, MO, US); Rocky cliff, Charcas-Vanegas road, *Lundell 5734* (ARIZ, LL, US); Concepcion del Oro, *Olsen 297* (LL); 5 mi W of Concepcion del Oro on road to Mazapil, *Olsen 300* (LL); 12 mi S of Cedros on dirt road, *Olsen 330* (LL); 7 mi E of Cedros on road to Mazapil, *Olsen 331* (LL); 2 mi E of Mazapil on road to Concepcion del Oro, *Olsen 332* (LL); Concepcion del Rio, *Palmer 314* (LL, MO, NY, UC, US); Open limestone slopes, *Pennell 17415* (MEXU, MICH, NY, US); 5 mi S of Rancho Mahoma, *Shreve 8579* (ARIZ, MICH, UC); Stony bajada near San Rafeal between Cedros and Camacho, *Shreve 9385* (ARIZ, MICH, UC).

Zaluzania mollissima is a frequent shrub on rocky limestone slopes and along cliffs; it is also found on sandy clay soils in open disturbed areas of the Chihuahuan Desert. It is sympatric with *Z. triloba* and occurs within a few miles of *Z. augusta* var. *augusta.* Common associates include: *Larrea tridentata* and species of *Acacia, Atriplex, Euphorbia* and *Opuntia.*

As pointed out earlier, *Zaluzania mollissima* is most closely related to *Z. augusta* and *Z. subcordata,* as evidenced by their pappose ray florets, entire, densely pubescent leaves and shrubby habit. The most distinguishing characteristic of this taxon is its long ray florets (more than 1 cm), not seen in any other *Zaluzania* taxon. It is suggested that the triploid *Z. mollissima* is an apoendemic element in the genus, derived from a *Z. augusta*-like ancestor.

5. **Zaluzania subcordata** W. M. Sharp, Ann. Missouri Bot. Gard. **22:** 111. 1935. Type: MO!. *Purpus 2580.* MEXICO: **Puebla.** On rocky hills of Esperanza, Aug 1907 (Isotypes: F!, GH!, MEXU!, NY!, UC!, US!).

Perennial shrubs to 3 m in height. Stems glabrous at base to tomentose above. Roots without fleshy tubers. Leaves cordiform, margins entire to minutely crenate; upper leaves 1.8–3.1 cm long, 0.6–1.4 cm wide; lower leaves 5.5–6.0 cm long, 2.4–3.4 cm wide;

pubescence of the upper surface tomentose, lower surface lanate; petioles 0.5–1.4 cm in length, densely pubescent. Peduncles 0.7–1.8 cm long, pubescent. Heads 1.1–1.2 cm in diameter (including the rays). Involucre 2-seriate, the bracts lanceolate, outer series 3.3–3.7 mm long, 1.5–1.7 mm wide; inner series slightly shorter and broader. Pales oblanceolate, weakly trifid, 3.2–3.5 mm long, 0.6–0.9 mm wide. Ray florets 8–10, ligules yellow, 3-lobed, 4.8–5.1 mm long, 4.2–4.5 mm wide; throat glabrous, style branches well exserted. Disc florets ca 40, yellow, corolla 2.5–2.9 mm long, 1.4–1.7 mm wide; throat pubescent. Ray achenes with a few hairs along the ridges; 1.7–1.9 mm long, 0.5–0.6 mm wide; pappus of two small awns or scales. Disc achenes 1.4–1.8 mm long, 0.5–0.7 mm wide. (Figure 9).

REPRESENTATIVE SPECIMENS. MEXICO. **Puebla:** Esperanza, *Arsene 7093* (US); Below Atzizintls (San Antonio), *Balls 5318* (GH, UC, US); 7 mi N of Esperanza on road to Ciudad Serdan, *Olsen 291* (LL); Hills about Esperanza, *Pittier 452* (US); Atzitzuilta, *Purpus 2790* (UC); In the vicinity of San Luis Tultitlanapa, near Oaxaca, *Purpus 3027* (ARIZ, F, MO, NY, UC, US); Coxcaltan, *Purpus 4121* (UC). **Vera Cruz:** Mt. Orizaba, *Seaton 286* (F, NY, US).

Zaluzania subcordata is restricted to the rocky limestone hills in southeastern Puebla and adjacent Vera Cruz. It is interpreted as an apoendemic element and is most closely related to *Z. augusta* and *Z. mollissima*.

6. **Zaluzania augusta** (Lag.) Sch.-Bip. Flora **44:** 562. 1861.
(Typification and synonymy cited under varietal names.)

Perennial shrubs to 3 m in height. Stems glabrous at base to puberulent above. Roots without fleshy tubers. Leaves ovate to ovate-lanceolate, apex rounded or acute, margins entire or glandular crenate; upper leaves 1.2–1.8 cm long, 0.2–0.6 cm wide; lower leaves 4.2–7.5 cm long, 1.7–4.0 cm wide; pubescence of the upper surface hirsute to tomentose, lower surface lanate; petioles up to 1.0 cm in length. Peduncles 1.0–2.3 cm in length, puberulent. Heads 0.8–1.5 cm in diameter (including the rays). Involucre 2–3 seriate; the bracts lanceolate, outer series 3.0–3.3 mm long, 0.7–0.8 mm wide; inner series nearly equal in length, but slightly broader. Pales 3.5–3.7 mm long, 0.5–0.8 mm wide. Ray florets 8–10, ligules yellow, 2–3 lobed, 5.0–6.3 mm long, 2.5–3.0 mm wide; throat glabrous;

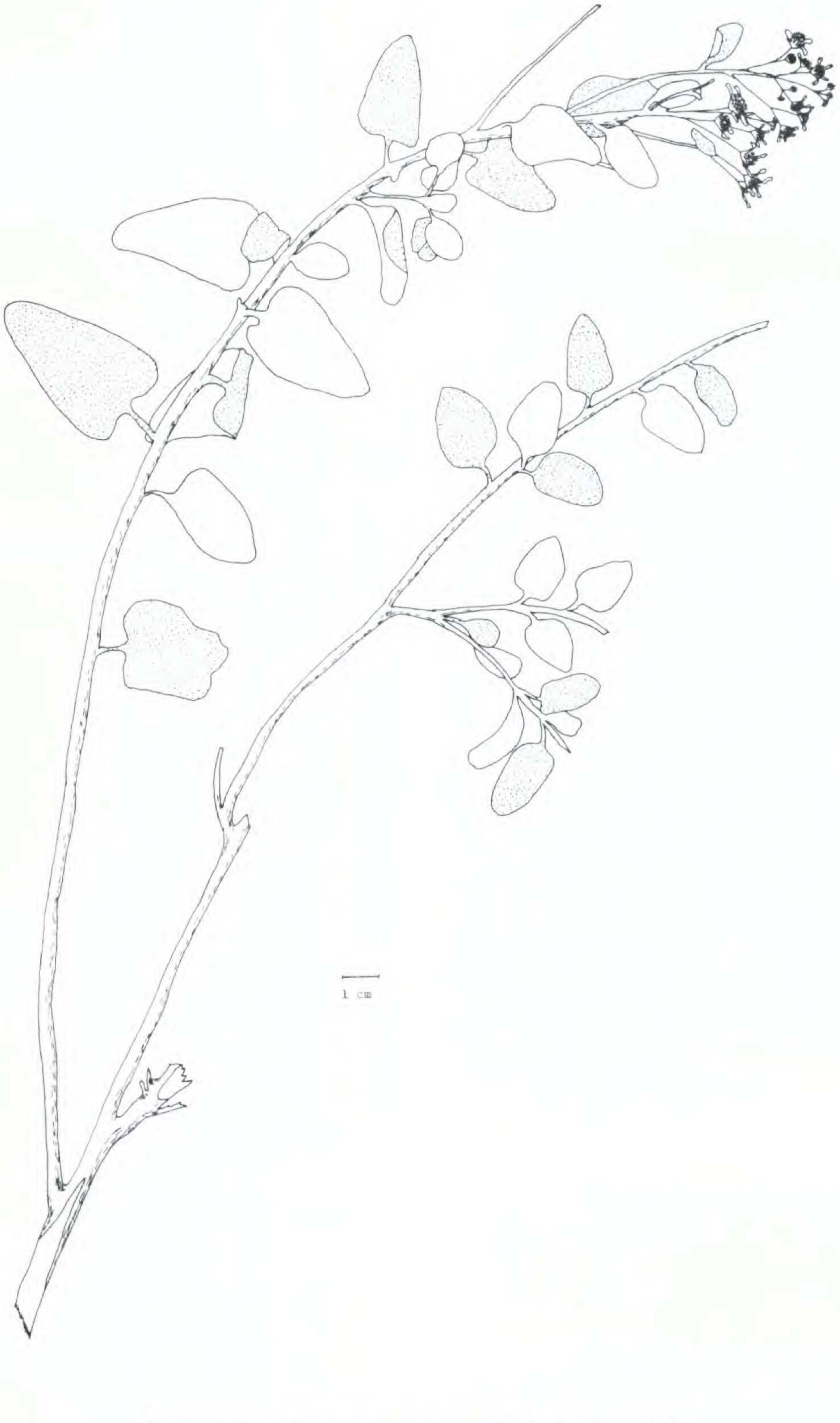

Figure 9. *Zaluzania subcordata,* habit tracing.

styles well exserted from the tube. Disc florets ca 50, corolla yellow, 2.5–2.8 mm long, 1.0–1.2 mm wide; throat glabrous. Ray achenes glabrous, 1.4–1.8 mm long, 0.6–0.8 mm wide; pappus of several (usually 4) scales or absent. Disc achenes 1.8–2.0 mm long, 0.6–0.8 mm wide.

KEY TO THE VARIETIES

a. Surface of the leaf dark green above, gray beneath; leaf apex acute; ligules 2-lobed; pappus of the ray florets of 4 scales; pales glutinous. .... 6a. var. *augusta* (Figure 10)

a. Surface of the leaf gray on both sides; leaf apex rounded; ligules usually 3-lobed; pappus of the ray florets reduced to 2 scales or absent; pales pubescent. .... 6b. var. *rzedowskii* (Figure 11)

6a. **Zaluzania augusta** (Lag.) Sch.-Bip. var. **augusta**

Ferdinanda augusta Lag., Gen & Sp. Nov. Pl. **31.** pl. 2. 1816. No type designated and herbarium at MA was destroyed. Photograph at GH! taken by Blake in 1925 of specimen he believed may have been seen by Lagasca, now deposited at P.

Anthemis lutescens La Llave & Lexarza, Nov. Veg. Desc. **1:** 26. 1824. MEXICO: **Federal District.** Guadalupe Mountains. *Cervantes s.n.*, w/o date. Description only, no specimens cited.

Chrysophania fastigiata Kunth ex Less., Syn. Gen. Comp. **224.** 1832. TYPE: P. *Humboldt s.n.*, w/o date. MEXICO: **Hidalgo.** Actopan.

Ferdinanda lutescens (La Llave & Lexarza) DC., Prodr. **5:** 553. 1836. Microfiche, G-DC!

Zaluzania angusta Sch.-Bip., *in* Hemsl. Biol. Centr. Am. Bot. **2:** 159. 1881. An orthographic variant of the original Lagasca name.

Zaluzania augusta var. *augusta,* while very common over much of its range, often becomes dominant in parts of Guanajuato and Queretaro where it frequently covers the low limestone hills. It can be found at elevations of 1500–2500 m on dry open slopes, upon stone-walled hedgerows between cultivated fields and on rocky limestone outcrops generally. Associated taxa include *Acacia, Agave, Jatropha, Mimosa, Opuntia* and *Prosopis.*

It is not unusual to find var. *augusta* heavily grazed by grasshoppers and other insects which consume the leaves late in the growing season, but there is generally no insect damage to the young plants at other times.

Variety *augusta* is a highly variable taxon, especially in its leaf morphology. Leaf shape varies from small, elliptic leaves with entire margins to large, nearly triangular leaves with crenate margins. (Figure 10).

REPRESENTATIVE SPECIMENS. MEXICO. **Aguascalientes:** Hwy to Ojuelos, Jalisco 9 mi E of Aguascalientes, *McVaugh & Koelz 69* (MICH); 15 km al NE de Aguascalientes, sobre la carretera a Loreto, *Rzedowski 25095* (LL, MICH). **Federal District:** Valley de Teotihuacan, *Conzatti 3413* (MEXU); Sierra de Guadalupe, *Miranda 572* (MEXU); Lomas de Chapultepec, *Miranda & Barkley 16M954* (F, LL); Hills near Mexico, *Pringle 7415* (MO). **Guanajuato:** San Luis de la Paz limite de los Estados Guanajuato y San Luis Potosi, *Hernandez 132* (MEXU); Frequent in Satae, *Kenoyer 1705* (NY); 35 mi E of Guanajuato on Hwy 110 to Dolores Hidalgo, *Olsen 271* (LL); 6 mi NE of Dolores Hidalgo on Hwy 110, *Olsen 272* (LL). **Hidalgo:** 2.5 mi W of Huichapan, *Cronquist 9617* (GH, LL, MICH, MO, NY, US); 2 km al NW de Tepeapulco, *Jimenez 226* (ASU, MICH); Zimapan, *Kenoyer A168* (F); 7 km al NE de Pachuca sobre

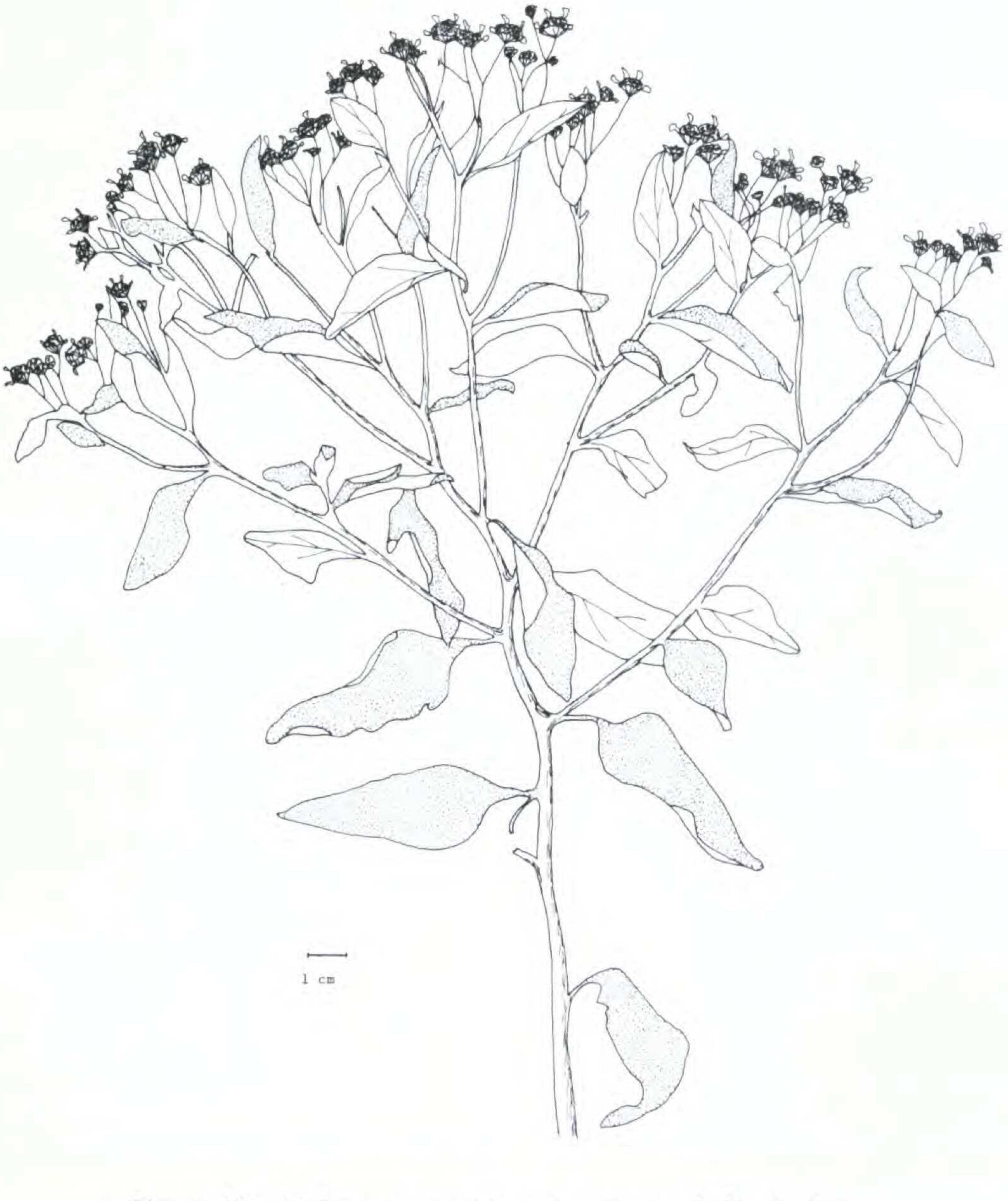

Figure 10. *Zaluzania augusta* var. *augusta*, habit tracing.

la carretera Pachuca-Mineral del Chico, *Moreno 162* (MICH, NY); 10 mi E of Hidalgo-Queretaro border on Hwy 45, *Olsen 284* (LL); 2.5 mi N of Pachuca on Hwy 105 to Real del Monte, *Olsen 286* (LL); Hills near Tula, *Pringle 9996* (F, GH, LL, MO, NY, US); Pachuca, *Purpus 1539* (F, GH, MO, NY, UC); Cerro Banxu, 4 km al N de Orizabita, *Quintero 3134* (MICH); Between Pachuca and Real del Monte, *Rose & Painter 6675* (NY, US); San Gregorio, municipio de San Tepeapulco, *Rzedowski 16965* (US); Huichapan, *Steyermark 52280* (F); W slopes of Cerro Chulco, near Rancho Los Voladores, 5 km SW of Apan, *West C-21* (MICH). **Jalisco:** Between Lagos de Morena and Aguascalientes, *Templeton 802e* (NY). **Mexico:** Vertiente E del Cerro Gordo, cerca San M. de las Piramides, *Cisneros 255* (MICH); 53 mi NW of Mexico City and 54 mi SE of San Juan del Rio, *Cronquist 10522* (LL, NY, US); Polotitlan, *Matuda 26371* (MEXU, NY); Sierra de Guadalupe, *Matuda 29525* (NY); Rio Hondo Canyon, *Pringle 3144* (F, GH, MICH, MO, NY, UC, US); Lecheria, *Pringle 13091*(F, GH, MICH, MO, NMC, US); Near Guadalupe, Valley of Mexico, *Rose & Painter 7278* (US); 2 km al W de Tlalnepantla, *Rzedowski 15854* (MICH); Laderos orientalis del Cerro Gordo, ca de San Martin de las Piramides, *Rzedowski 18834* (LL, MEXU, MICH). **Michoacan:** Dry west facing slopes in former *Acacia-Opuntia* thorn scrub above Rancho las Cerquillas at km 11 on Mex Hwy 120, halfway between Uruetaro and Alvaro Obregon ca 22 km NE Morelia, *Iltis & Cochrane 249* (US). **Morelos:** Xochitepec, *Lyonnet 844* (LL). **Queretaro:** Entre Cadereyta and Vizarron, *Altamirano 1652* (US); Cerro de las Campanas, *Arsene 10065* (F, GH, MO, US); 10 km al N de Queretaro, sobre la carretara a San Luis Potosi, *Crespo 345* (MICH); Cadereyta, *Kelly 669 & 669a* (UC); Hwy 57, 2 mi SE of San Juan del Rio, *Olsen 242* (LL); 8 mi from Hwy 57 on Hwy 45 to Pachuca, *Olsen 243* (LL); 6 mi S of Vizarron on Hwy 120, *Olsen 283* (LL); 4.7 mi N of Queretaro on Rt 57, *Rock M433* (LL). **San Luis Potosi:** 40 mi S of San Luis Potosi on Hwy 57, *Olsen 274* (LL); 2 km E de San Jose Alberquerque, municipio de Santa Maria del Rio, *Rzedowski 8431* (LL).

6b. **Zaluzania augusta** (Lag.) Sch.-Bip. var. **rzedowskii** McVaugh, Contr. Univ. Mich. Herb. **9:** 464. 1972. TYPE: MICH! *McVaugh 17673*. MEXICO: **Zacatecas:** Rocky oak covered hill ca 25 km E of Huejuquilla el Alto near the road between Valparaiso, Zacatecas and Mezquitic, Jalisco. 4–5 Sep 1958.

REPRESENTATIVE SPECIMENS. MEXICO. **Durango:** 87 km N of Durango, *Cronquist 10775* (GH, LL, MEXU, MICH, NY, US); 2–4 mi W of Nombre de Dios *Gentry 8437* (GH, MICH, UC). **Guanajuato:** Steep rocky hills ca 10 km SW of Leon, road to San Francisco del Rincon, *McVaugh 24275* (MICH). **Jalisco:** Near village of Arroyos del Agua, 10 km NW of Huejuquilla del Alto, *Feddema 2377* (LL, MICH, MO, NY); ca 11 mi SE of Lagos de Moreno, near Hwy to Leon, *McVaugh 13246* (MICH, US); Arroyos del Agua, 10 km NW de Huejuquilla, *Rzedowski 17629* (ARIZ, LL, MICH, NY). **Zacatecas:** 15 mi by road E of Huejuquilla del Alto on road leading from San Antonio to N-S road from Valparaiso to Mexquitic, Jalisco, *Anderson & Laskowski 3623* (MICH, NY).

Variety *rzedowskii* differs from var. *augusta* primarily in leaf characters, as noted in the key. It occurs primarily on clay soils,

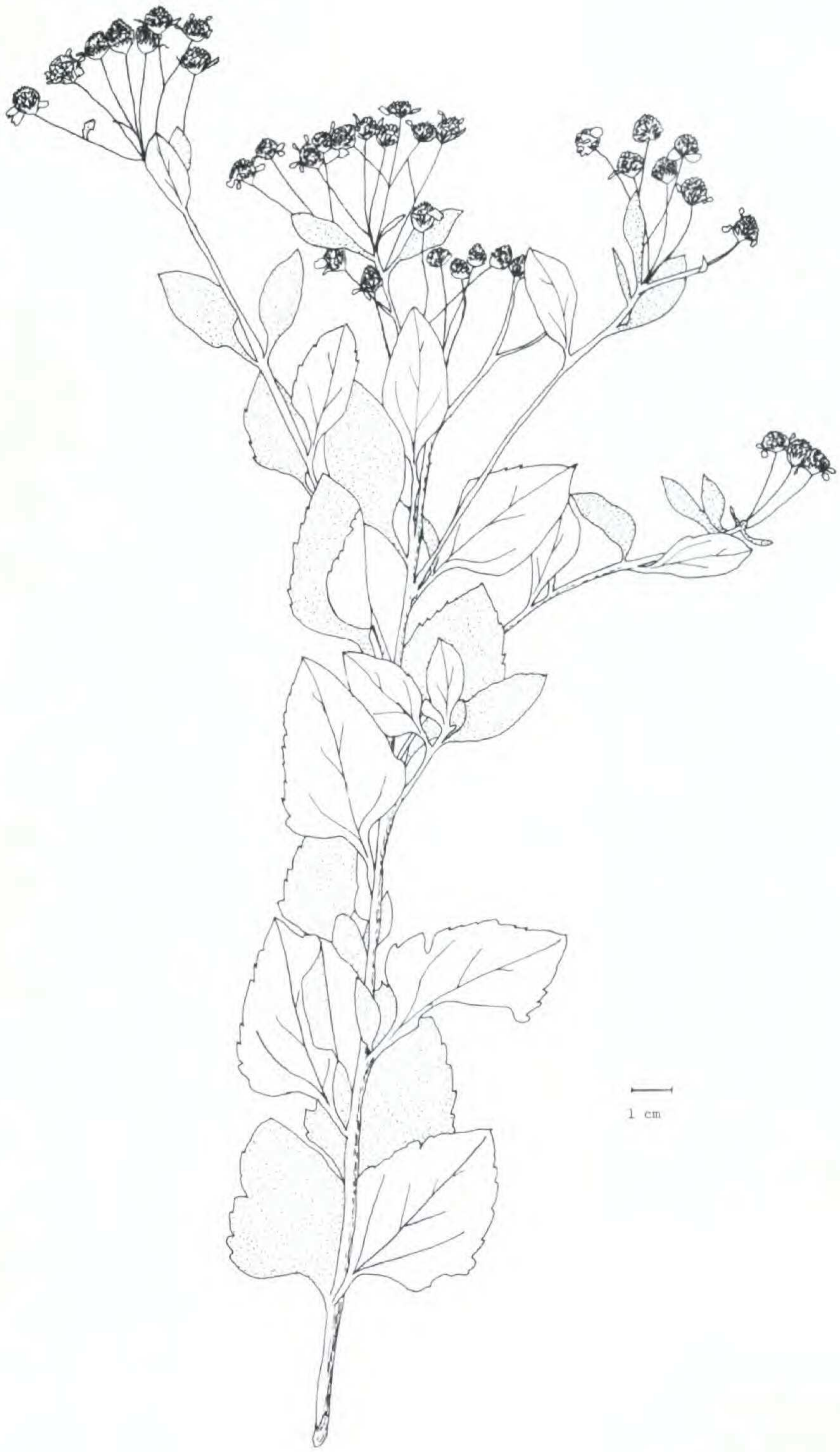

Figure 11. *Zaluzania augusta* var. *rzedowskii,* habit tracing.

stony pastures, and high shrub grasslands at elevations of 1500–2000 m. Associated taxa include *Bursera, Quercus,* and cacti.

Populations of var. *rzedowskii* from the northern part of its range are typically erect and unbranched, as opposed to the shrubby habit of the more southern populations. This unbranched habit makes these populations resemble superficially the herbaceous perennial taxa, *Zaluzania megacephala* and *Z. discoidea,* although the pappus and pubescent pales of var. *rzedowskii* serve to distinguish readily between them. The convergence in habit seen in these taxa may represent a similar response to external factors such as moisture or exposure; alternatively, it may reflect a common genetic component linking the shrubby taxa with the herbaceous perennial taxa.

One questionable collection, *Cronquist 10775,* has been tentatively assigned to this variety. The pubescence of the upper leaf surface is not whitish as typically found in this taxon and the ligules are only 2-lobed, but the geographic locality (N of Durango), ray pappus of two scales and the pubescent pales suggest placement in var. *rzedowskii.*

7. **Zaluzania pringlei** Greenm., Proc. Amer. Acad. **39:** 101. 1903. TYPE: GH! *Pringle 8710.* MEXICO: **Morelos.** Limestone hills near Jojutla. 18 Oct 1902 (Isotypes: F!, MO!, NY!, UC!, US!).

Perennial shrubs to 3 m in height. Stems glabrous at base becoming puberulent above. Leaves elliptic to ovate, margins glandular-crenate; upper leaves 2.5–3.7 cm long, 0.8–1.5 cm wide, lower leaves 7.4–7.9 cm long, 3.4–3.6 cm wide; pubescence of the upper surface pustulate, lower surface hirsute; petioles 0.5–2.2 cm in length. Peduncles 0.5–1.3 cm long, puberulent. Heads 0.7–1.6 cm in diameter (including the rays). Involucre 2-seriate, the bracts lanceolate; outer series 3.0–3.2 mm long, 1.2–1.3 mm wide, inner series nearly equal. Pales 3.2–3.3 mm long, 1.6–1.7 mm wide. Ray florets present or absent, 1–5, ligules white, 4.5–4.8 mm long, 3.0–3.3 mm wide; throat pubescent, style branches well exserted from the tube. Disc florets ca 50, corolla white, 2.4–2.6 mm long, 2.0–2.4 mm wide; throat pubescent. Ray achenes glabrous, 1.3–1.5 mm long, 0.5–0.7 mm wide, pappus absent. Disc achenes 1.9–2.2 mm long, 0.5–0.8 mm wide. (Figure 12).

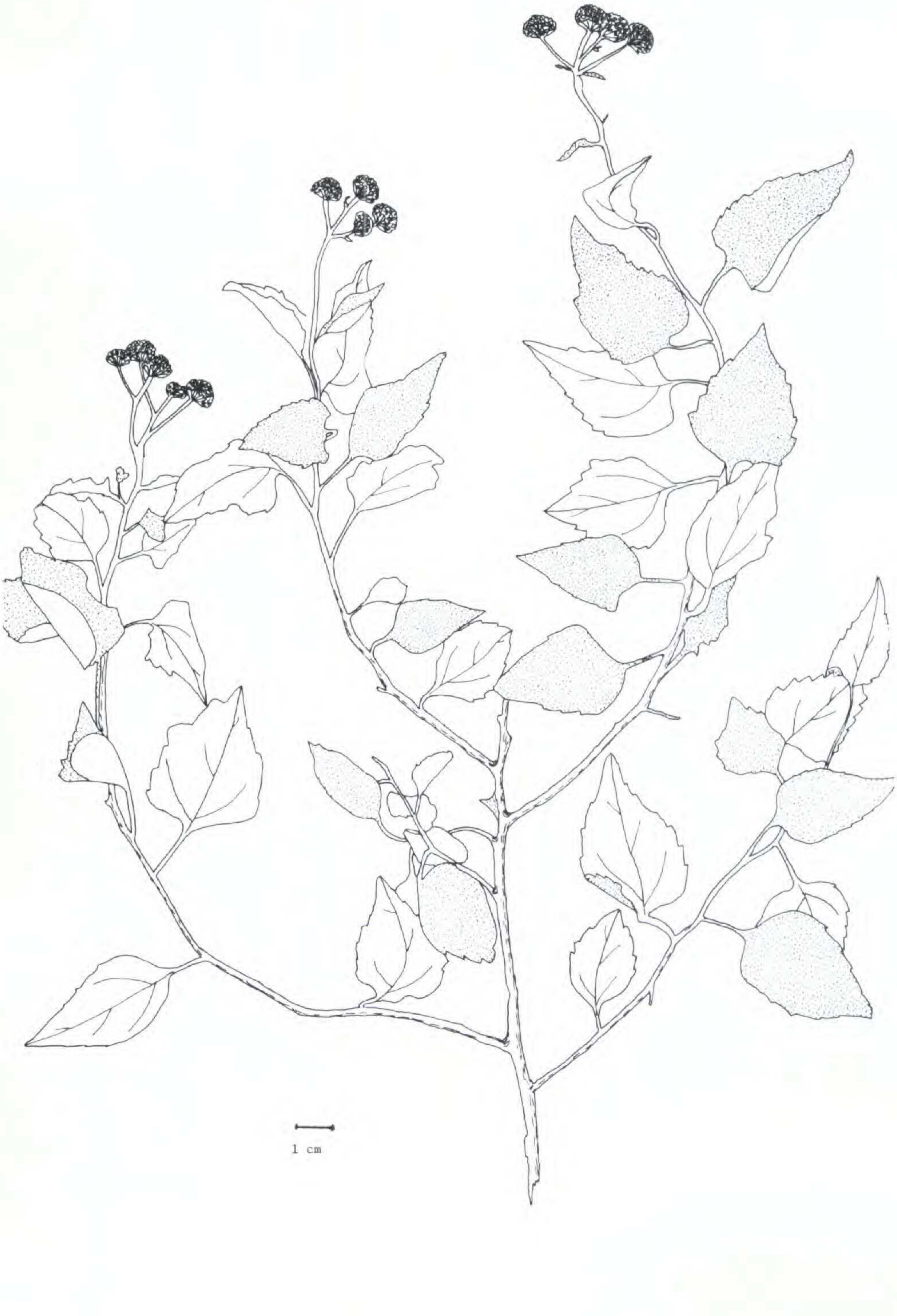

Figure 12. *Zaluzania pringlei*, habit tracing.

REPRESENTATIVE SPECIMENS. MEXICO. **Guerrero:** Steep calcareous, brushy E slope, overlooking N end of Chilpancingo, *Cronquist 9718* (LL, MEXU, MICH, NY); 8 mi N of Chilpancingo on Hwy 95 to Acapulco, *Olsen 395* (LL); 3 mi N of Chilpancingo, *Olsen 396* (LL). **Morelos:** 10 km N de Tehuxtla, *Gomez-Pompa 1070* (MEXU). **Puebla:** Along the Pan American Hwy, about 17 road mi SE of Acatlan and about 3 mi SE of Petlacingo, *Cronquist 9696* (GH, LL, MICH, MO, NY, US); Calcareous rocky hills 20–25 km SE of Acatlan, *McVaugh 24001* (MICH).

Zaluzania pringlei is a frequent shrub on calcareous brushy slopes at elevations of 1000–1600 m. It typically is found in subtropical deciduous forests associated with *Acacia, Bursera, Eysenhardtia,* and cacti.

Greenman (1903), presumably because of its usual discoid nature, believed it most closely related to *Zaluzania discoidea.* In my opinion, *Z. pringlei* is allied more closely to the shrubby taxa centering around *Z. montagnifolia,* as evidenced by its ovate, pustulate (on the upper surface), glandular-crenate leaves, shrubby habit, and geographic range. It is clearly distinguished from the latter taxon by floral characters, especially its white corollas.

8. **Zaluzania montagnifolia** (Sch.-Bip.) Sch.-Bip., Flora **44:** 563. 1861. TYPE: P. *Muller 293.* MEXICO: **Vera Cruz:** Between Veracruz and Orizaba. 1857 (Phototype, F!, Fragment, F!).

Ferdinanda montagnaefolia Sch.-Bip., Koch's Berl. Allgem. Gartenz. **179.** 1858.

Zaluzania asperrima Sch.-Bip. var. *asperrima,* Flora **47:** 218. 1864. TYPE: P. *Liebmann 544.* MEXICO: **Puebla:** Chapulco. Oct 1841 (Isotype GH!; Phototypes F!, GH!, NY!).

Zaluzania asperrima Sch.-Bip. var. *montagnaefolia* (Sch.-Bip.) Rob. & Greenm., Proc. Amer. Acad. **34:** 532. 1899.

Perennial shrubs to 4 m in height. Stems glabrous at base becoming hirsute above. Roots without fleshy tubers. Leaves elliptic to ovate, margins crenate, may be glandular, decurrent along the petiole; upper leaves 2.4–4.6 cm long, 1.1–1.7 cm wide, lower leaves 7.4–9.3 cm long, 3.6–4.7 cm wide; pubescence of the upper surface pustulate, lower surface puberulous to tomentose; petioles 1.0–2.0 cm in length. Peduncles 0.9–2.3 cm in length. Heads 1.5–2.0 cm in diameter (including the rays). Involucre 2–3 seriate, the bracts lanceolate, 4.0–4.2 mm long, 1.4–1.6 mm wide, the inner series slightly shorter and broader. Pales 3.4–3.5 mm long, 1.4–1.6 mm wide. Ray florets 6–10, ligules yellow, 6.6–6.9 mm long, 4.5–4.8 mm wide; throat minutely pubescent, style branches well exserted from the tube. Disc florets ca 50, corolla yellow, 2.5–2.7 mm long, 1.7–2.1

mm wide; throat pubescent. Ray achenes glabrous, 1.8–2.0 mm long, 0.4–0.7 mm wide; pappus absent. Disc achenes glabrous, 1.4–1.7 mm long, 0.5–0.8 mm wide. (Figure 13).

REPRESENTATIVE SPECIMENS: MEXICO: **Guerrero:** 9 mi W of Chilpancingo on road to lumber town of Olmiltemi, *Anderson & Laskowski 4347* (F, GH, MICH, MO); 9 mi W of Chilpancingo, *Cronquist 9716* (GH, LL, MICH, MO, US); ca 15 mi SE of Tonatico, *Webster & Brackon 16200* (F, MICH). **Morelos:** Tepozatlan-Chalci, *Paray 1712* (MEXU). **Oaxaca:** Mex. Hwy 190, 25 mi SE of Oaxaca, ca 1 mi S of road to Mitla, *Anderson & Laskowski 4197* (F, GH, MICH); Cerro de Frujano, distrito del Centro, *Conzatti 2317* (F); Cuesta de Huauchilla, Distrito de Wochixtlan, *Conzatti 4253* (US); Magdelena Feitfrac, Distrito de Tlacolula, *Conzatti 4601* (US); Talatlaco, *Conzatti 4812* (LL); 8 mi S of Ejutla and 47 mi S of Oaxaca, *Cronquist & Sousa 10441* (GH, LL, MICH, US); Monte Alban, near Oaxaca, *Pringle 4928* (GH, MEXU, MICH, MO, NY, UC, US); Monte Alban, cerca de la ciudad de Oaxaca, *Rzedowski 19279* (LL, MICH); Monte Alban, near Oaxaca city, *Smith 612(631)* (LL, MICH, MO, NY, UC, US). **Puebla:** 10 km by road S of Esperanza on road to Morelos Canada and Tehuacan, *Anderson & Anderson 5320* (MICH); 31 mi NW of Tehuacan, *Cronquist & Sousa 10378* (GH, LL, MEXU, MICH, US); Tehuacan, *Holway 5347* (GH); Open fields along rt 150, ca 1 mi N of Tehuacan, *King 2645* (LL, MICH, UC, US); Along Hwy 150d to Orizaba, *Olsen 245* (LL); ca 4 mi S of Esperanza on Mex 28 to Tehuacan, *Olsen 246* (LL); 4 mi S of Esperanza, *Olsen 247* (LL); 10 mi N of Tehuacan, *Olsen 248* (LL); 16 mi N of Tehuacan on Hwy 190 to Puebla, *Olsen 249* (LL); ca 30 mi S of Esperanza along Mex 28 to Tehuacan, *Olsen 365* (LL); Along Hwy 125, ca 3 mi S of Acatepec, *Olsen 367* (LL); In the vicinity of San Luis Tultitlanapa, near Oaxaca, *Purpus 2530* (GH, MO, NY, UC, US); Barrancas near Tlanisloltepec, *Purpus 3823* (GH, MO, NY, UC, US); Rocky soils, Tlacuilaltepec, *Purpus 3824* (GH, MO, NY, UC, US); Tehuacan, *Purpus 5610* (F, MO, UC); Near Tehuacan, *Rose & May 5947* (US); 2 km al SE of Tehuacan sobre la carretera a Caxcatlan, *Rzedowski 28154* (MICH). **Vera Cruz:** 3 mi NE of Acultzingo, *Cronquist & Sousa 10352* (GH, LL, MICH, US); Orizaba, *Kenoyer A173* (F).

Zaluzania montagnifolia is a locally common shrub in south-central and southeastern Mexico at elevations of 1500–2200 m. It is relatively low and spreading in the northern part of its range, becoming taller and less highly branched to the south. *Zaluzania montagnifolia* occurs on dry calcareous soils, frequently along rocky hillsides. Associated taxa include: *Acacia, Agave, Bursera, Juniperus, Pinus, Prosopis,* and *Quercus.*

Zaluzania montagnifolia is the central element in a group of shrubby, epappose taxa. It is most closely related to *Z. pringlei* and *Z. sodiroi,* as evidenced by its vegetative morphology, habit and distribution; however, it is easily distinguished from the former by its yellow florets, and from the latter by its pustulate upper leaf surface.

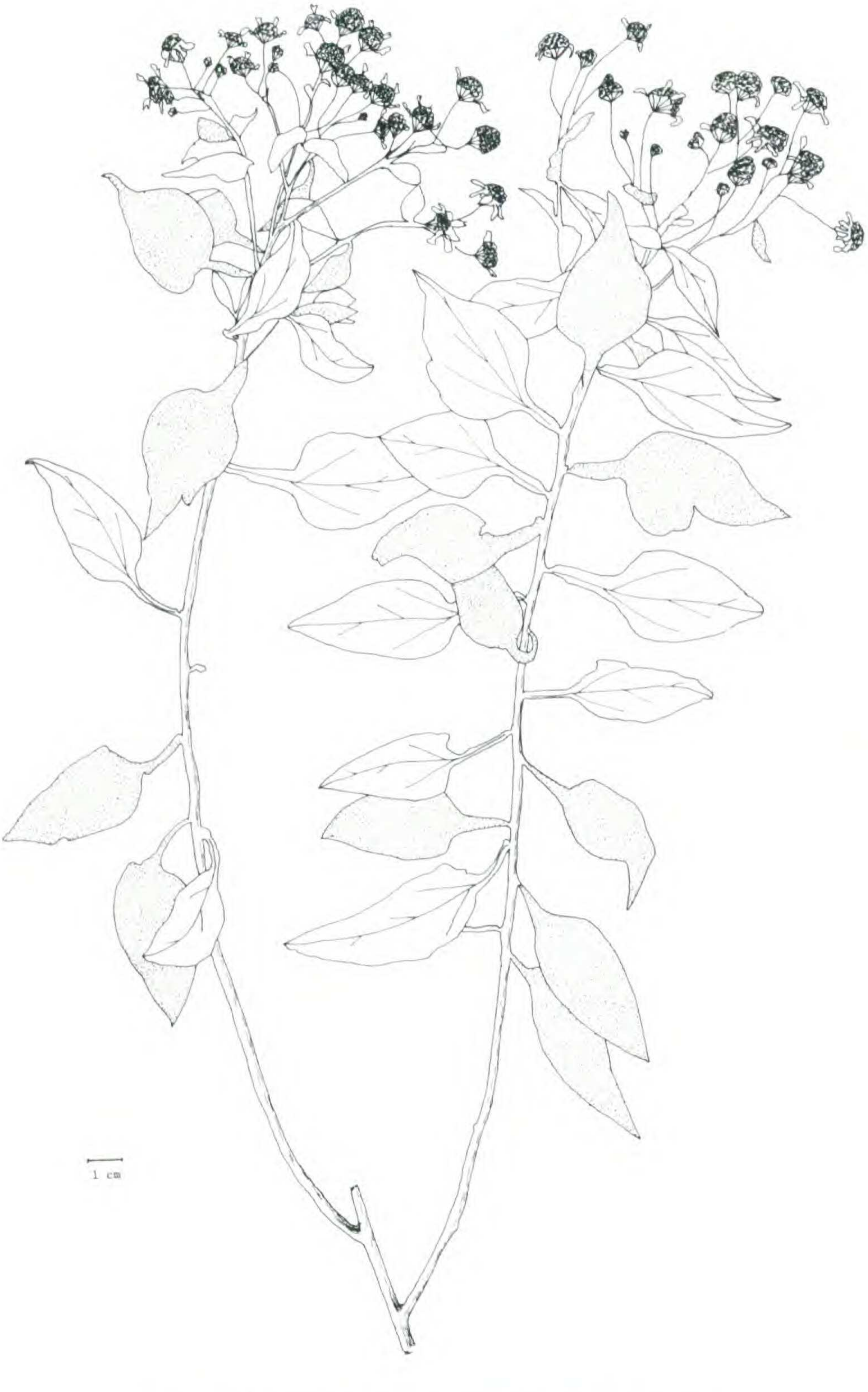

Figure 13. *Zaluzania montagnifolia*, habit tracing.

9. **Zaluzania sodiroi** Hieron., *In* Engl. Bot. Jahrb. **29:** 35. 1900. TYPE: B. *Sodiro 31/1.* ECUADOR: Arid inter-Andean hills, w/o date (Phototype, F!; Isotype fragment, US!).

Zaluzania nonensis Hieron., *In* Engl. Bot. Jahrb. **29:** 36. 1900. TYPE: B. *Sodiro 31/2.* ECUADOR: Near Nono, in silvis subandinis, w/o date (Phototype F!, NY!).

Zaluzania quitensis Hieron., *In* Engl. Bot. Jahrb. **29:** 37. 1900. TYPE: B. *Sodiro 31/3.* ECUADOR: In hills near Quito, w/o date (Phototype F!, NY!; Isotype fragment, US!).

Monactis subdeltoidea Robinson, Proc. Amer. Acad. **47:** 210. 1911. TYPE: B. *W. Jameson 162.* ECUADOR: on the banks of the Machangara River, near Quito, 2750 m, 21 Jan 1856 (Isotype fragment, US!).

Kingianthus sodiroi (Hieron.) H. Robinson, Phytologia **38:** 415. 1978.

Perennial shrubs to 3 m in height. Stems puberulent at base to tomentose above. Roots without fleshy tubers. Leaves ovate, margins glandular-dentate, upper leaves 2.9–4.7 cm long, 0.6–1.5 cm wide, lower leaves 7.6–11.5 cm long, 3.7–6.7 cm wide; pubescence of the upper surface hirsute, lower surface tomentose; petioles 0.5–1.9 cm in length. Peduncles 0.3–1.0 cm long, tomentose. Heads 1.1–1.5 cm in diameter (including the rays). Involucre 2-seriate, the bracts lanceolate, outer series 2.9–3.5 mm long, 1.0–1.4 mm wide, inner series longer with the same width. Ray florets 8–10, ligules yellow, 6.2–6.5 mm long, 3.2–3.5 mm wide; throat glabrous, style branches well exserted from the tube. Disc florets ca 20, corolla yellow, 2.7–3.1 mm long, 1.0–1.3 mm wide; throat glabrous. Ray achenes glabrous, 2.7–3.1 mm long, 0.6–0.8 mm wide; pappus absent. Disc achenes glabrous, 1.8–2.0 mm long, 0.6–0.7 mm wide. (Figure 14).

REPRESENTATIVE SPECIMENS. ECUADOR: Vicinity of Quito, Cotocollao, *Asplund 6116* (NY, US); Machachi, *Asplund 6246* (NY, US); North rim of the valley of the Rio de Canar, between Tambo and Suscal, *Camp & Giler E-2785* (US); Entre la Magdelena y Chillogallo, *Firmin 140* (US); Hacienda S. Gridro, entro la Magdelena y Chillogallo, *Firmin 471* (LL, US); Quito, *Holway & Holway 948* (US); In coll. y Chimbia, prp. Quito, *Mille 568* (MO); Guapalo, roadside E of Quito, *Olsen & Escobar 419* (LL); In roadside waste areas across from Administration de Aduanas, Pan American Hwy km 6.5, *Olsen & Escobar 435* (LL); Along Pan American Hwy N of Machachi, *Olsen & Escobar 485* (LL); Ficoa, near Ambato, *Pachano 134* (US); Quito, *Sodiro 568* (NY); Entre Pangala y Alao, Prov. Chimborazo, *Solis 7591* (F); Valle Seco del Pedregal, cord. Oriental, *Solis 8439* (F); De Cunchibama a Tangaleo, Prov. Tungurahua, *Solis 8594* (F); Chimbacalle, Quito, *Solis 10104* (F); Shanshipamba, Prov. Imbabura, *Solis 14254* (F); Shanshipamba, Pena Blanca, *Solis 14448* (F); Magotilla-Magota, Prov. Pichincha, *Solis 16514* (F); Valley of Lloa, about 6 km WSW of Quito overlooking the Rio Cinto, *Ugent & Ugent 5594* (US).

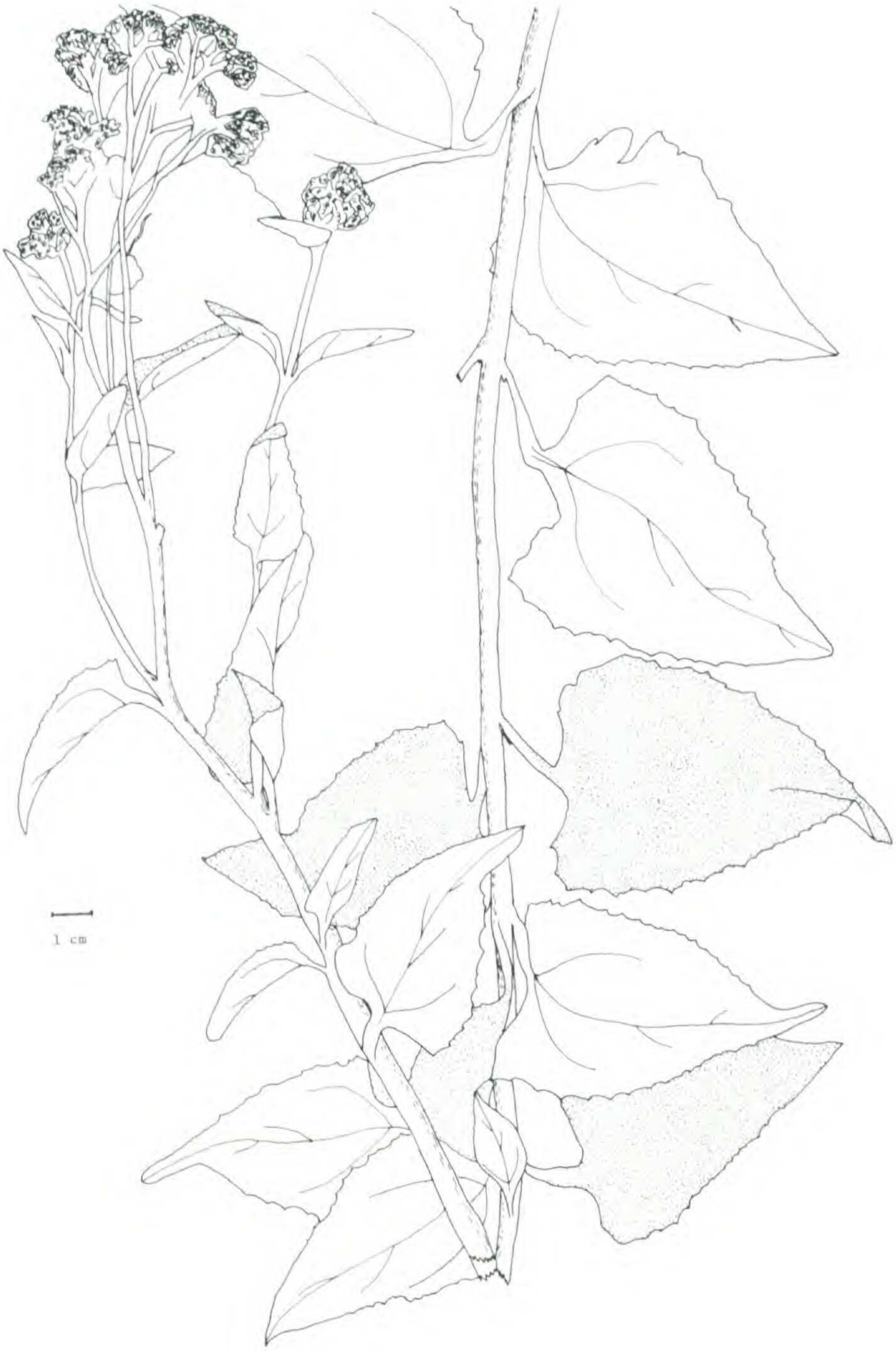

Figure 14. *Zaluzania sodiroi*, habit tracing.

Zaluzania sodiroi occurs as a roadside shrub in the high grasslands of Ecuador at elevations of 2300–3200 m. Associated taxa include: *Castilleja, Passiflora, Rumex, Senecio, Solanum,* and bamboo.

Zaluzania sodiroi presumably arose as a chance introduction into Ecuador, probably from a *Z. montagnifolia*-like ancestor. *Z. sodiroi* differs from other *Zaluzania* taxa in producing one unusual flavonoid compound (Olsen, 1977) as well as the usual set of glycosides. On paper chromatograms, this compound has previously only been seen in *Calea;* however, the floral morphology and alternate leaves in *Z. sodiroi* clearly distinguish it from *Calea.*

The recently published monotypic genus *Kingianthus* (Robinson, 1978), erected to house *Zaluzania sodiroi,* is certainly not sufficiently distinct to warrant exclusion from *Zaluzania.* Robinson believes this taxon related to *Monactis* rather than to *Zaluzania,* based on his interpretation of micromorphological characters. In my opinion, the taxon in question is correctly placed in *Zaluzania.* The $n = 18$ chromosome number and the *Zaluzania* flavonoid pattern (Olsen, 1977) clearly distinguish it from *Monactis* ($n = 30$ and a very different flavonoid pattern) and strongly support its inclusion in *Zaluzania.*

EXCLUDED TAXA

Zaluzania, Comm. ex Gaertn. f. Fruct. **3:** 74. 1805. Name invalid when published.
=*Bertiera* Aubl. Pl. Gui. **1:** 180. 1775. Rubiaceae.

Zaluzania anthemidifolia Rob. & Greenm. Proc. Amer. Acad. **34:** 531. 1899.
=*Hybridella anthemidifolia* (Rob. & Greenm.) Olsen, Madrono **24:** 29. 1977.

Zaluzania ensifolia Sch.-Bip. Flora **47:** 216. 1864.
=*Viguiera ensifolia* Blake, Contr. Gray Herb. **54:** 58. 1918.

Zaluzania globosa (Ort.) Sch.-Bip. var. **globosa,** Flora **44:** 564. 1861.
=*Hybridella globosa* (Ort.) Cass. var. *globosa,* Dict. Sci. Nat. **22:** 86. 1821.

Zaluzania globosa var. **myriophylla** (Sch.-Bip.) Sharp, Ann. Missouri Bot. Gard. **22:** 103. 1935.
=*Hybridella globosa* var. *myriophylla* (Sch.-Bip.) Olsen, Madrono **24:** 29. 1977.

Zaluzania grayana Rob. & Greenm. Proc. Amer. Acad. **34:** 531. 1899.
=VIGUIERA TRILOBA (Gray) Olsen, *comb. nov.*

Gymnolomia triloba Gray, Proc. Amer. Acad. **17:** 217. 1882. TYPE: GH! *Lemmon 846.* Arizona. Mountains of southern Arizona, south of Rucker's Valley. 1881.

Zaluzania grayiana Rob. & Greenm. Proc. Boston Soc. Nat. Hist. **29:** 104. 1899. An orthographic variant.

Zaluzania indica Reinw. ex Blume, Mus. Bot. Lugd. Bat. **1:** 239.
=*Geniostoma rupestre* Forst., Char. Gen. **24:** 12. 1776. Loganiaceae.

Zaluzania oppositifolia Sch.-Bip., Flora **44:** 562. 1861.
=*Calea scabrifolia* Benth. & Hook., Gen. Pl. **2:** 391. 1873.

Zaluzania pinnatilobata Sch.-Bip., Flora **47:** 219. 1864.
=*Viguiera pinnatilobata* (Sch.-Bip.) Blake, Contr. Gray Herb. **54:** 95. 1918.

Zaluzania resinosa S. Wats., Proc. Amer. Acad. **21:** 388. 1886.
=*Greenmaniella resinosa* (Watson) Sharp, Ann. Missouri Bot. Gard. **22:** 141. 1935.

Zaluzania squarrosa Sch.-Bip., Flora **47:** 216. 1864.
=*Viguiera squarrosa* (Sch.-Bip.) Blake, Proc. Amer. Acad. **49:** 376. 1913.

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DEPARTMENT OF BOTANY
SOUTHWESTERN AT MEMPHIS
MEMPHIS, TENNESSEE
38112